Leeuwin Current Symposium 2007

Proceedings of a Symposium held in September 2007
convened by A Pearce (Curtin University of Technology)

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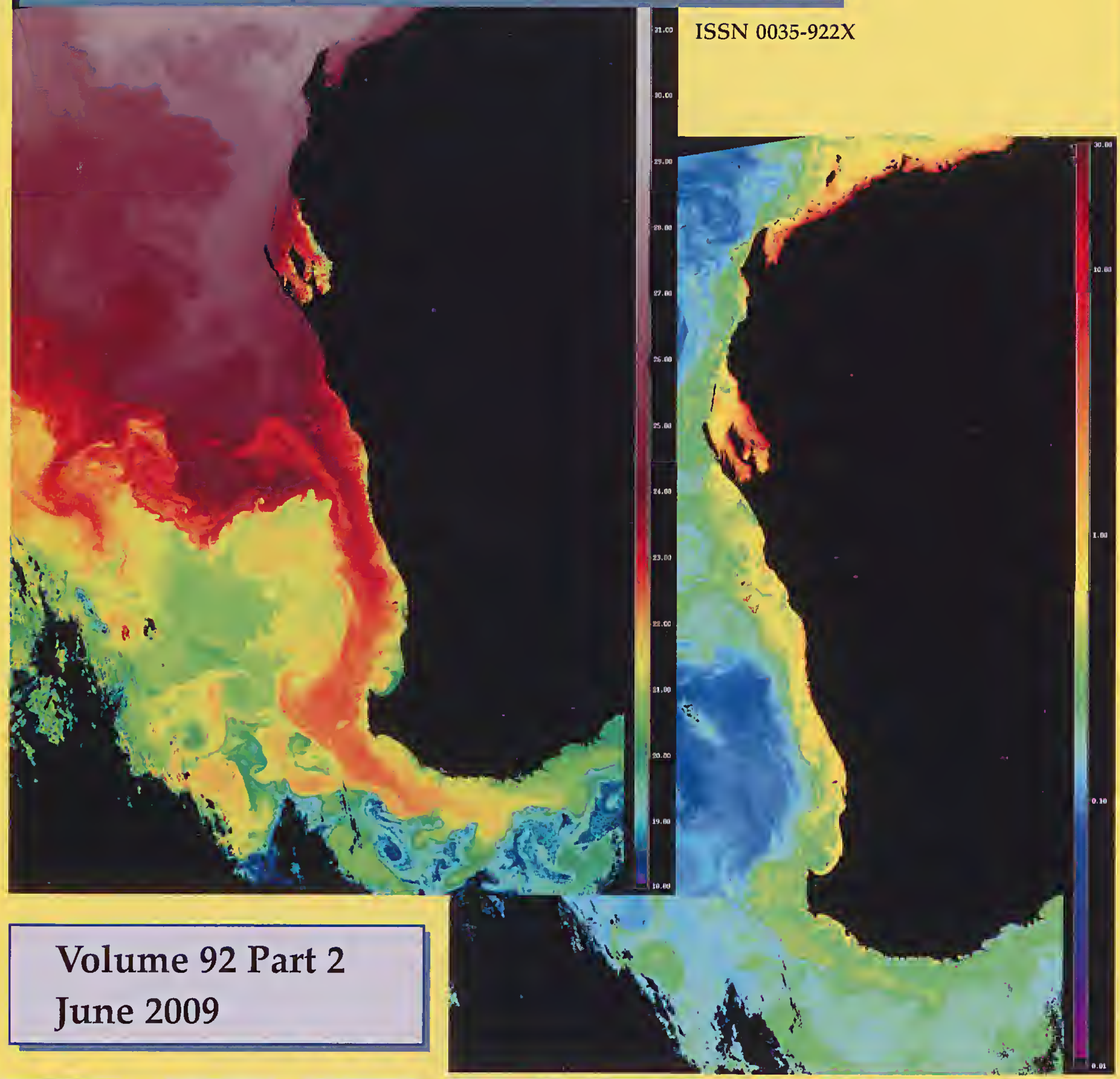

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Front cover: Satellite images of the Leeuwin Current on 7th May 2009, showing the sea-surface temperature (°C, on the left) and the chlorophyll concentration (mg/m^3, on the right) derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua sensor. The black patchy areas in the lower left corner are clouds. Images produced by Peter Fearns, Curtin University of Technology.

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HONORARY EDITOR'S FOREWORD

Following the successful Leeuwin Current Symposium held in 1991, published as a Special Issue in the Journal of the Royal Society of Western Australia as Volume 74, in September 2007, a one-day Symposium on the Leeuwin Current was held at the University of Western Australia. Convened by Alan Pearce, the objective of this latter Symposium was to report on the progress that had been made and research that had been undertaken in the previous 16 years, based on the increase in field surveys and theoretical studies. The papers deriving from the latter Symposium are presented in this Special Issue – The Leeuwin Current 2007 Symposium.

As a part of its mission to promote Science, The Royal Society of Western Australia committed to producing this Special Issue which would promote a general community and scientific awareness of the Leeuwin Current and its importance ecologically, and assist in the dissemination of the information presented at the Symposium. All the papers have undergone the normal peer review process, but have been tailored to appeal to a general scientific community as well as to a specialised audience, and are a stand alone collection of papers covering the key issues associated with the Leeuwin Current. The Symposium programme included general reviews of the history of the Leeuwin Current, the oceanography of the Current in various geographic zones, multi-disciplinary case studies linking the Leeuwin Current with the biology and ecology of the marine area related to the Current, and the fish and fisheries associated with the Current.

The cover of the Symposium Issue presents two expressions of the Leeuwin Current: both are satellite images of the Leeuwin Current, with one showing the sea-surface temperature and the other, chlorophyll concentration.

The Symposium was sponsored by The Royal Society of Western Australia in association with the Western Australian branch of the Australian Marine Sciences Association, the Australian Meteorological and Oceanographic Society, the University of Western Australia, the Western Australian Marine Sciences Institute, and Murdoch University, and this support is gratefully acknowledged. I would also like to thank the Sub-editor, Margaret Brocx, for the enormous work in assistance and administration involved in the publication of this Volume.

Kathy Meney
Honorary Editor
The Royal Society of Western Australia

PREFACE

Dr Steve Blake,

CEO Western Australian Marine Science Institution (WAMSI)

It is with great pleasure that I write this Preface for the Proceedings of the Leeuwin Current Symposium 2007.

The 1991 Leeuwin Current Symposium, sponsored by the Royal Society of Western Australia some 16 years earlier, was the first one-day Symposium that presented a synthesis of understanding at that point in time, based on a range of previous research initiatives commencing as early as 1897. A significant amount of additional inter-disciplinary work was undertaken on the Leeuwin Current in the following years and it was considered that a second Leeuwin Current Symposium should be organised, again sponsored by the Royal Society of Western Australia, to highlight our improved understandings.

The Symposium, held in September 2007 at the University Club of WA, was a huge success with over 100 people attending. The Symposium Organising Committee comprised: Alan Pearce (Convenor; Curtin University of Technology); Bruce Buckley (Chairman, WA branch of the Australian Meteorological and Oceanographic Society AMOS); Euan Harvey (University of Western Australia); Gary Kendrick (University of Western Australia); Phil O'Brien (President, Royal Society of WA); Valerie Pearce, Jane Rosser (Royal Society of WA); and Mike van Keulen (Chairman, WA branch of the Australian Marine Sciences Association AMSA) and are all to be congratulated on their efforts to organise the Symposium and subsequently bring together this exciting range of papers on the Leeuwin Current.

The Leeuwin Current influences nearly every facet of marine research in Western Australia, bringing warm water southwards down the Western Australian coast from the tropics, but equally remarkable is it's influence as far away as Tasmania. This conveyor belt that skirts the edge of the continental shelf from the Pilbara coast south, provides an easy ride for many tropical species who subsequently colonise areas off the West Coast bioregion and even beyond the Capes region. But it is more complex than that, with eddies being spawned off the main current causing mechanisms to enhance shelf and offshore productivity, including larval fish distributions. The discovery of the seasonal and interannual variations in the strength of the Leeuwin Current and its associated offshore eddy field, being stronger in winter than in summer and also in *La Nina* years compared with *El Nino* periods; and the linkage with the annual settlement of the puerulus stage of the western rock lobster, represent one of WA marine science's major success stories. Not only does it provide a high degree of predictability to WA's major western rock lobster fishery, but it further demonstrates the importance of combining a range of marine science disciplines: oceanography, marine remote sensing, fisheries biology, marine ecology etc. around a common uniting theme, the poleward flowing western boundary current, known today as the Leeuwin Current.

A new era of research has now commenced on the Leeuwin Current; its likely response and impacts in terms of predicted climate change effects. Whatever the changes, the Leeuwin Current will continue to have a fundamental impact on WA's marine biodiversity and the way we use the coastal oceans in the coming decades. Our understanding and monitoring of the Leeuwin Current will therefore remain a cornerstone of WA marine scientific endeavour for years to come.

The Symposium Proceedings have successfully built on our previous understandings and integrated a collection of scientific research papers representing many of the most recent advances in our understanding of the Leeuwin Current and its influence on the marine life of Western Australia. I congratulate the paper authors and all those involved with the Proceedings, on furthering our scientific knowledge of this, "the" most important WA boundary current.

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Introduction: Some historical "milestones" in the Leeuwin Current, and the Leeuwin Current Symposium 2007

A Pearce

Convenor; Curtin University of Technology

With this second Symposium focussing on the Leeuwin Current and its influence on the oceanography and marine biology off Western Australia, it is enlightening to look back at some of the key events/papers from the earliest speculations about the current system off our coast. It is only 3 decades since George Cresswell "discovered" and formally named the Leeuwin Current, yet in the relatively short time since then its unusual (and in many ways unique) characteristics have invoked ongoing local and international interest.

This brief introductory review traces some of the "milestones" which (in the author's opinion) have spelt out significant advances in our understanding of the structure, behaviour and significance of the Leeuwin Current system. As such, it provides an update to the historical review by Cresswell (1991) in the Proceedings of the first Leeuwin Current Symposium held in 1991.

Biological pioneers: Saville-Kent (1897) and others

Although early current charts showed a northwards boundary current off Western Australia, the fisheries biologist William Saville-Kent (1897) realised that there must in fact be a warm southerly flow to explain his observations of tropical marine species at the Abrolhos Islands and the large difference in (winter) temperature between the waters around the Islands and those at the adjacent mainland coast. Subsequent studies of the distribution of marine fauna and flora along the coast (*e.g.*, Michaelsen 1908; Dakin 1919) both confirmed and extended Saville-Kent's conjectures.

Rafts of warm surface water: Gentilli (1972)

An analysis of Indian Ocean sea-surface temperature charts by the geographer Joseph Gentilli (1972) revealed that there was a progression in the timing of the warmest water down the Western Australian coast. The warmest month on the Northwest Shelf was January, with the warm water progressively spreading southwards by April over a large area in the eastern Indian Ocean southward to (but offshore of) Shark Bay, with an isolated patch off Cape Leeuwin also in April. He attributed the presence and movement of these "rafts" to an inflow from the western Pacific Ocean, and sketched the southward movement of warm water down the Western Australian coastline.

New technologies and the naming of the Leeuwin Current: Cresswell & Golding (1980)

A major study of the larval stages of the western rock lobster during the mid-1970s coincided with the development of new oceanographic technologies. Self-recording current meters were deployed for periods of days to weeks at a number of sites on the outer continental shelf between the Abrolhos Islands and Rottnest Island (Cresswell *et al.* 1989) – these were the first *in situ* current meter measurements off south-Western Australia and indicated a seasonal change in the alongshore current direction. Satellite-tracked free-drifting buoys were also being developed at this time (Cresswell 1978), and the trajectories of a number of buoys released off the Western Australian continental shelf (Cresswell 1980) clearly revealed the complexity of the eddying southward stream and its easterly extension from Cape Leeuwin into the Great Australian Bight. Also at this time, satellite oceanography was just emerging as an operational reality, and early sea-surface temperature (SST) images of Western Australian waters showed the band of warm water and the associated eddy field (Legeckis & Cresswell 1981).

With this now conclusive evidence of the existence and nature of the southward flow, Cresswell & Golding (1980) formally named the Leeuwin Current.

Large-scale forcing of the Leeuwin Current: 1984–85

Following Thompson's (1984) suggestion that the southward flow (against the prevailing, and upwelling-favourable, wind system) could be caused by an anomalously strong alongshore pressure gradient, Godfrey & Ridgway (1985) used steric height and wind data to show the seasonal balance of forcing along the shelf break. They attributed seasonal changes in the meridional sea level gradient off Western Australia to the flow of Pacific Ocean water into the equatorial Indian Ocean through the chain of Indonesian islands.

The Leeuwin Current Interdisciplinary Experiment (LUCIE): 1986–87

Originally conceived as a multi-disciplinary survey of the Leeuwin Current, LUCIE evolved into a detailed oceanographic study of the current system in 1986/87, comprising research cruises complemented by current moorings along and across the continental shelf and slope (Boland *et al.* 1988). These were the first year-long direct current and hydrographic measurements across the Leeuwin Current, confirming the presence of the large alongshore geopotential gradient and providing further insight into the dynamics of the flow (Church *et al.* 1989; Smith *et al.* 1991).

Sealevel & ENSO relationships, and the rock lobster: 1986–88

The progression of the seasonal sea level cycle down the west coast and across the Great Australian Bight was linked with the Leeuwin Current by Pariwono *et al.*

(1986), who also suggested an association with *El Nino*/Southern Oscillation (ENSO) events. Pearce & Phillips (1988) in turn showed that annual settlement of the puerulus stage of the western rock lobster is highly correlated with the strength of the Leeuwin Current: during ENSO years, annual mean sea level is relatively low (implying a weak Leeuwin Current) and puerulus settlement is poor compared with *La Nina* periods.

Feng *et al.* (2003) have since quantified the association between sea level and the Leeuwin Current transport, and ENSO/Leeuwin Current links with other Western Australian commercial fisheries were subsequently shown by (*inter alia*) Lenanton *et al.* (1991) and Caputi *et al.* (1996).

Modelling studies: 1986 –

There have been corresponding advances in both theoretical and numerical modelling of the Leeuwin Current system. By including thermohaline forcing in a linear stratified model of the circulation in the southeastern Indian Ocean, McCreary *et al.* (1986) were able to reproduce the alongshore steric height gradient and eastward geostrophic flow presented by Godfrey & Ridgway (1985) and so force a poleward surface boundary current against the prevailing winds. The equatorward undercurrent was also represented.

Batteen & Rutherford (1990) developed the first numerical model with sufficient spatial and temporal resolution to depict the generation and general properties of the Leeuwin Current and the associated eddy field – the results agreed well with the 1986/87 LUCIE current meter observations. Domingues *et al.* (2007) subsequently used a particle tracking technique to reveal links between the various sources of the Leeuwin Current and the regional circulation.

The Leeuwin Current Symposium: 1991

A one-day symposium held in 1991, sponsored by the Royal Society of Western Australia with invited speakers addressing pre-selected topics, attempted to summarise the existing state of knowledge and understanding of the geology, physics, meteorology and biology of the Leeuwin Current. The set of 13 papers (Pearce & Walker 1991) included comparisons between the climates, oceanography and biology of the eastern boundary current systems in the southern Pacific, Atlantic and Indian Oceans (the Humboldt, Benguela and Leeuwin Currents respectively). There was also a focus on the role played by the Leeuwin Current on the fisheries, corals, seagrasses and seabirds along the Western Australian coast.

New satellite technologies (altimeter and ocean colour): 1990s –

The advent of operational satellite altimetry (primarily TOPEX/Poseidon from 1992) provided for the first time global surface ocean currents on a regular basis at eddy-resolving temporal and spatial scales (*e.g.*, Fang & Morrow 2003; Feng *et al.* 2005), leading to the ability to model larval transport processes (Griffin *et al.* 2001) and ultimately to web-based ocean currents charts and the Bluelink ocean forecasting website (http://www.bom.gov.au/oceanography/forecasts/).

Similarly, the launch of SeaWiFS in August 1997 provided for the first time direct remote sensing measurements of marine biological processes on an operational basis, yielding near-surface chlorophyll concentrations from satellite ocean colour observations (Moore *et al.* 2007). Clark & Li (2004) subsequently used satellite altimetry to show that the onshore geostrophic transport associated with the alongshore steric height gradient is enhanced during *La Nina* periods and may contribute to the observed inter-annual variability in puerulus settlement.

Focused multi-disciplinary research vessel surveys: 2000s

A series of multi-disciplinary cruises undertaken by the University of Western Australia and CSIRO on the FRVs *Franklin* and *Southern Surveyor* examined the dynamics of the Leeuwin Current and associated shelf circulation. Covering the southwestern and south coasts, complemented by repeated transects off Two Rocks during the Strategic Research Fund for the Marine Environment (SRFME – Keesing *et al.* 2006), these surveys described the seasonal water properties, circulation and some aspects of the biology along the continental shelf and in the Leeuwin Current. The dominant current systems and physical water properties along the coast have been summarised by Woo & Pattiaratchi (2008) and Pattiaratchi & Woo (2009). The seasonal biophysical characteristics of the Ningaloo and Capes regions were covered in detail by Hanson *et al.* (2005a, 2005b) and Woo *et al.* 2006, while the repeated SRFME transects clearly demonstrated how seasonal changes in the chlorophyll maximum layer are linked with the annual strengthening of the Leeuwin Current (Koslow *et al.* 2008).

The Leeuwin Current and its eddies: DSR Special Issue 2007

Details of the physical and biological structure of the Leeuwin Current and the offshore eddy field were described in a dedicated volume of Deep-Sea Research in 2007 ("The Leeuwin Current and its eddies": Waite *et al.* 2007). Results from research cruises were supplemented by a series of modelling papers to show the dynamic interactions between the Leeuwin Current, the Leeuwin Undercurrent and both warm-core and cool-core eddies, and the spatio-temporal variability of primary production along the shelf.

The Leeuwin Current 2007 Symposium

At this stage of the journey, we have been able to build on the advances made over the past few years and take a fresh look at the state of knowledge of the Leeuwin Current system, bringing together some of the recent research on the unique marine environment off Western Australia.

This special issue of the Journal of the Royal Society of Western Australia is complementary to the DSR 2007 volume by incorporating a series of reviews and some new results about the continental shelf oceanography and biology associated with the Leeuwin Current. The papers are published largely in the sequence in which they were presented at the Symposium. One orally-presented paper has been withdrawn, another has been split into two, and a third has been converted from a poster to a written paper. The first paper examines the evolution of, and long-term changes in, the "Leeuwin Current" over geological time-scales, suggesting that the southward flow (as we know it) was probably well established 2 to 3 million years ago (Wyrwoll *et al.* 2009), but recognising that indirect evidence of warmer waters in the geological past may not necessarily have been associated with a proto-Leeuwin Current *sensu stricto*. Fluctuations in the Leeuwin Current in response to plate reorganisation, tectonics and climate variability have resulted in major shifts in ocean temperature and sea levels along the Western Australian coast, with some of the responses to past changes providing possible guides to the response of the Leeuwin Current to anticipated future climate states.

This is followed by a series of papers reviewing the larger-scale oceanography from the source region(s) in the north, down the west coast and eastwards towards the Great Australian Bight.

The source waters of the Leeuwin Current in the far north are shown by D'Adamo *et al.* (2009) to originate from the tropical Pacific Ocean via the Indonesian Archipelago, together with a contribution from the northern Indian Ocean, both these sources being warm and relatively low in salinity. The Leeuwin Current itself assumes its identity as a strong poleward boundary current south of North West Cape. Some previously unpublished current meter measurements taken by MetOcean Engineers and the Australian Institute of Marine Science along the North West Shelf between 1995 and 2007 have been presented for the first time. The "Holloway Current" is the title proposed for the south-westward flow along the outer North West Shelf in honour of a deceased colleague who made major contributions to the oceanography of this region.

Two papers review the physical and biological oceanography along the west coast between Exmouth and Cape Leeuwin. The main current systems and accompanying water properties are addressed by Pattiaratchi & Woo (2009), defining the geography and seasonality of the Leeuwin Current (strongest in autumn/winter), the Leeuwin Undercurrent (the northward current underlying the Leeuwin Current) and the wind-driven Capes and Ningaloo Currents which flow northwards along the inner continental shelf in summer. The authors define 8 water masses on the basis of their temperature/salinity/oxygen characteristics, with the Leeuwin Current itself largely being a combination of Tropical Surface Water and South Indian Central Water.

Feng *et al.* (2009) describe the seasonal and inter-annual variations in the strength of the Leeuwin Current and its associated offshore eddy field, these being stronger in winter than in summer and also in *La Nina* periods compared with *El Nino* years. By complementing satellite-derived chlorophyll-a data with shipboard measurements, biophysical mechanisms relating to variability of the ocean production off the west coast are examined. The important issue of the potential effect of long-term climate change on ocean production off the west coast is also addressed, with present evidence pointing to a probable reduction in the flow of the Leeuwin Current under more *El Nino*-like conditions in the future.

In a neat mix of oceanographic history, modern current measurements and numerical modelling, Cresswell & Domingues (2009) describe the seasonal influx of warm, low-salinity Leeuwin Current waters from the west coast around Cape Leeuwin and their subsequent penetration eastwards along the south coast of Western Australia. Westward of the Recherche Archipelago, current speeds of up to 1.8 m/s have been measured just off the shelf although they weaken further into the Great Australian Bight. Both cyclonic and anti-cyclonic eddies abound and (together with the winds) play a major role in the observed variability of the current system along the south coast.

Two papers on fish and fisheries off Western Australia complete the large-scale overviews.

Beckley *et al.* (2009) comprehensively review a variety of previous studies of larval fishes between the North West Shelf and the Great Australian Bight. Larval fish assemblages within the Leeuwin Current are found to be largely a mixture of oceanic, slope, tropical and temperate coastal species, with strong seasonal variability in species composition reflecting these different sources as well as seasonal changes in the strength and location of the Leeuwin Current.

Previously described relationships between the Leeuwin Current and recruitment to a variety of Western Australian commercial invertebrate and scalefish fisheries are re-examined by Lenanton *et al.* (2009). The close link between the strength of the Leeuwin Current and settlement of the puerulus phase of the western rock lobster has been confirmed, with some dependence on other factors such as water temperature and possibly ocean productivity (chlorophyll-a) and eddy kinetic energy. While environmental variables remain within historical ranges, the relationship between the Leeuwin Current and western rock lobster is likely to be maintained. Under these circumstances, and in the longer-term, weakening of the Leeuwin Current in response to an increasing frequency of *El Nino* events may result in lower puerulus settlements in future years. Most other fisheries (for example, scallops, whitebait and salmon) are essentially inshore-dwelling species which have exhibited varying responses to oceanographic factors such as the Leeuwin and Capes Currents, and coastal salinity, which is most likely a surrogate for some physical or biological factor that influences survival of larvae and newly settled juveniles.

A series of more regional studies dealing with aspects of the oceanography and biology of key areas follow: the Ningaloo reef system, the Houtman Abrolhos Islands, Rottnest Island, the Geographe Bay/Capes area and Esperance.

The unexpectedly high productivity of the Ningaloo Reef coastal area is attributed by Hanson & McKinnon (2009) to episodic regional upwelling driven by the seasonal north-flowing Ningaloo Current, enhancing nutrient concentrations along the inner shelf. During *El Nino* years in particular, primary production is greatly elevated but this is not necessarily reflected in copepod abundance; higher up the food chain, on the other hand, whale sharks are more abundant during *La Nina* periods with a strong Leeuwin Current than during *El Ninos*.

The biota at the Abrolhos Islands are addressed in a series of 3 papers dealing with the marine flora, fish and birds in the Island groups.

Phillips & Huisman (2009) compare the marine plants (both seagrasses and seaweeds) at the Islands with those along the mainland coast at Jurien Bay, finding that the offshore assemblage represents a mix of tropical and temperate species (reflecting the tropical origins of the Leeuwin Current) while at the adjacent mainland coast the species are almost all temperate – reminiscent of Saville-Kent's original observations in the late 19th century.

Fish species over the 100-km latitude range of the Abrolhos Islands (Watson & Harvey 2009) are dominantly tropical, with much lower proportions of warm-temperate and sub-tropical species. The species composition is intermediate between those observed at Ningaloo (22°S) and Rottnest Island (32°S). While on this larger spatial scale the distribution can be attributed to the Leeuwin Current, there is a high level of variation in the composition of fish assemblages within each location on a site to site basis. This small scale variability is likely a result of numerous factors, for example differences in habitat and food availability.

The Abrolhos Islands are a fertile breeding ground for seabirds such as the Lesser Noddy and Brown Noddy during spring and summer (Surman & Nicholson 2009). As their diet consists largely of larval fish, the Noddy breeding patterns and success reflect fluctuations in the abundance of fish which in turn appear to be linked to variations in the Leeuwin Current. During periods of weak Leeuwin Current (*El Nino* events), breeding is severely delayed and reproductive output is poor suggesting depleted prey fish abundance, while variations in other factors such as the nearshore current system and the offshore eddies may also have some influence on food availability. This long-term dataset may provide a valuable insight going forward into the changing dynamics of current systems and potential impacts upon seabirds along the Western Australian coast.

Further south, a detailed analysis of a year-long current meter mooring off Perth has yielded invaluable information of the temporal variability and vertical structure of the currents down the water column (Cresswell 2009). Winter current speeds peaked at 0.6 m/s (associated with the Leeuwin Current, although the main core of the flow was probably further offshore), while in summer the northward flow of the Capes Current was evident, with a maximum observed speed of 0.9 m/s. Wind played a dominant role in the direction of the currents, and there were considerable cross-shelf current excursions – with obvious implications for the cross-shelf transport of marine larvae.

Historical current measurements are analysed by Pearce & Hutchins (2009) to study seasonal and inter-annual variations in the recruitment of two tropical damselfish species into the shallow reefs at Rottnest Island. Based on the observed current speeds both on and off the shelf, the authors suggest that the higher southward speeds in the Leeuwin Current (rather than the weaker, reversing shelf current system) are required to transport pelagic larvae southwards from their spawning grounds at the Abrolhos Islands to Rottnest within their normal pelagic larval duration of about 3 weeks. Under favourable current conditions, larvae spawned at Shark Bay can reach Rottnest Island within the 3 week period.

Continuing southwards, the distributions of fish and algae in the Capes region (Westera *et al*. 2009) show relatively few fish species of tropical or subtropical origin. There is however a large component of fish species classified as subtropical-temperate (44%), in addition to the expected temperate species. These distributions, however, are not closely linked with water temperatures, and the authors conclude that the Capes region is part of a large biogeographical transition zone. Likewise, the bulk of marine algae are temperate, but southward and northward range extensions are attributed to the Leeuwin and Capes Currents.

The influence of the Leeuwin Current on the marine biota along the south coast (on both geological time-scales and in the present) shows a gradient in the relative proportions of subtropical, south-western endemic and southern temperate species from west to east (Kendrick *et al*. 2009). Examining the distribution of macroalgal assemblages in particular, the rich diversity and high local species turnover has been attributed largely (but not exclusively) to the Leeuwin Current.

A key feature of recent work on the Leeuwin Current system has been the interplay between the physics and the biology, with consequent benefits to our understanding of the dynamics of both. William Saville-Kent would have been interested to see how far we have come.

In conclusion, we are very grateful to our sponsors for making the Symposium possible: the Royal Society of Western Australia (chief sponsors and publishers), the Western Australian branch of the Australian Marine Sciences Association (AMSA), the Australian Meteorological and Oceanographic Society (AMOS), the University of Western Australia (UWA), the Western Australian Marine Sciences Institute (WAMSI) and Murdoch University. Some travel support for interstate PhD's and recent postgraduates was made available through the Australian Research Council Research Network for Earth System Science (ARCNESS). We are also indebted to Professor Alistar Robertson (Dean of the Faculty of Natural and Agricultural Sciences, UWA) for formally opening the Symposium, and to Dr Steve Blake (CEO of WAMSI) for the Preface to this volume.

Finally, the authors are thanked for contributing the set of excellent papers, despite their ongoing routine work loads.

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The palaeoceanography of the Leeuwin Current: implications for a future world

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Abstract

Long-term progressive changes of the Leeuwin Current are linked to plate and ocean basin 'geography' and Cenozoic global climates and palaeoceanography. Suggestions of the presence of a proto-Leeuwin Current as early as late Middle to Late Eocene times (*c.* 35–42 Ma) cannot be verified by the fossil record of the western margin of Australia. "Leeuwin Current style" circulation around Australia was certainly established by the early Oligocene, in response to palaeogeographic changes in the Tasman Strait. This, followed by tectonic reorganisation of the Indonesian Archipelago throughout the Miocene, provided a palaeogeographic setting, which by the Pliocene was essentially that of today. The subsequent history of the Leeuwin Current comprises climatically-induced changes operating over orbital and sub-orbital temporal scales. Specifically, the advent of Pleistocene-style climates, especially over the last 800 000 years, and their associated interglacial – glacial states provide the two end-member climate-ocean states that have characterised Leeuwin Current activity during that time. Indications of the nature of these contrasting states is provided by: (i) the Last Interglacial (*c.* 125 Ka) during which sea level was higher by some +4 m, and with higher sea surface temperatures (SSTs) clearly indicating a more 'active' Leeuwin Current; and (ii) the Last Glacial Maximum (21 Ka), during which sea level was some 130 m lower than today, resulting in massive shelf extensions along the coast of Western Australia, accompanied by reduced Indonesian Throughflow, lower low latitude SSTs and changes in the Western Pacific Warm Water Pool, and with these changes, possibly reduced Leeuwin Current activity. Sub-orbital scale fluctuations in current strength are driven by global climate change associated with El Niño – La Niña events as well as regional climatic changes driven by volcanism. These forcing mechanisms operate at time scales well within the reach of human experience, and provide important comparative data for predicting the response of the Leeuwin Current to climate change predicted for this century. Studies of the impact of changes in the vigour of the Leeuwin Current on shallow marine communities are in their infancy. Coupling climate models with geological analogues provide important research agenda for predicting the trajectory of future changes to the Leeuwin Current and their impacts on the marine biota of coastal Western Australia.

Keywords: palaeoceanography, Leeuwin Current, Last Interglacial, Last Glacial Maximum

Introduction

The geological history of the Leeuwin Current involves a combination of re-arrangements of global geography in terms of both the continent positions and associated plate tectonic changes, and a global climate regime which brought the Earth out of an essentially 'ice free' world into the present Ice Age. Presently, the Leeuwin Current is a relatively strong southward flow of warm, low salinity tropical water along the Western Australian coast – from near North West Cape to Cape Leeuwin and on to the Great Australian Bight (Cresswell 1991) – driven by a meridional steric high gradient. Given the Leeuwin Current's general controls, of a southward pressure gradient force balanced by northward wind stresses, we see the Leeuwin Current being driven by hemisphere-scale climate constraints, as

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well as itself having a possible impact on the climate regime of the western margin of Australia. With the predicted progression of the Earth into a warmer future climate setting, the Leeuwin Current will be placed in a world which is being steered away from the distinctive glacial-interglacial climate signature of the last *c.* 800 000 years (Loutre & Berger 2000; Archer & Ganopolski 2005). Given the importance of the Leeuwin Current in controlling marine biogeography in the region, understanding its likely response to these changes remains to be established. In this contribution we use the geological record to elucidate the range of states that the Leeuwin Current has been able to adopt over long-time scales – information that may prove helpful in constraining model predictions of future events.

The history of the Leeuwin Current over plate tectonic time scales

The long-term geological history of the Leeuwin Current is linked to the relative position and organisation of the Australian plate (*e.g.*, Li & Powell 2001) juxtaposed against changes in global ocean and atmosphere climates that characterise specific time periods within the last *c.* 30 myrs (see Zachos *et al.* 2001). In their overall function, two 'ocean-gateways' – the Indonesian Throughflow and the Tasmanian Gateway – are clearly of importance and their roles figure prominently in discussions of the early history of the Leeuwin Current.

Establishment of the Tasmanian Gateway

Shafik (1990) and McGowran *et al.* (1997) suggest an early presence of a "proto-Leeuwin Current" stemming from late Middle to Late Eocene time (35–42 Ma). They specifically relate this to a wider plate reorganisation and a new phase of seafloor spreading marked by Chron C19 (41–42 Ma). Along the Western Australian coast the Middle Eocene Merlinleigh Sandstone of the central Carnarvon Basin preserves a colonial coralline assemblage, which in combination with the associated mollusc assemblage, suggests warm ocean conditions off this part of the coast during that time (McNamara & Scott 1983). The distinctive Merlinleigh assemblage may represent an outlier of the Eocene Austral Indo-Pacific Province. However, it is not at all clear that its presence can be unequivocally attributed to the presence of a proto-Leeuwin Current, as it could simply be an expression of regional SSTs. The same doubt can be expressed with respect to the evidence presented by McGowran *et al.* (1997), whose palaeontological data support warm water along the margins of southern Australia during this time, but whether this necessarily implies the presence of a proto-Leeuwin Current remains an open question.

Recent studies of Middle-Late Eocene (Bartonian-Priabonian, 40.4–33.9 Ma) foraminifers (Haig & Mory 2003) and molluscs (Darragh & Kendrick 2008) from the southern Carnarvon Basin near Kalbarri, have found no evidence of significantly warm SSTs over that time. Affinities of the mollusc assemblage lie substantially with those of the later Eocene of temperate southern Australia. This inference is in accord with the absence from the assemblage of tropical and subtropical foraminifers (Haig & Mory 2003) and corals (Darragh & Kendrick 2008). Hence there is at present no compelling evidence for the presence of any Austral Indo-Pacific (*i.e.*, tropical) provincial fauna in the Kalbarri Eocene assemblage, nor any clear manifestation of what could be interpreted as an Eocene Leeuwin Current phenomenon. It should be noted that Haig & Mory (2003) state that the absence of tropical and subtropical species of foraminifera suggests a cooling trend over this interval, comparable with that noted for southern Australian waters by McGowran *et al.* (2000).

McGowran *et al.* (1997) make the claim of evidence for proto-Leeuwin Current activity at *c.* 33 Ma with additional evidence of activity later in the Oligocene. These claims and those of an earlier (Eocene) existence of a proto-Leeuwin Current have to be seen within the context of more recent work on the timing of the opening of the Tasmanian Gateway, which facilitated flow along the southern margins and into the Pacific. Stickley *et al.* (2004) demonstrate that it was only after 30.2 Ma that the region saw the establishment of stable, open-ocean, warm-temperate, oligotrophic settings characterised by siliceous-carbonate ooze deposition. The evidence presented by the authors indicates that deepening of this early Oligocene Tasmanian Gateway initially produced an eastward flow of relatively warm surface waters into the southwestern Pacific Ocean, for which they also adopted the term "proto-Leeuwin" Current. It now seems clear that the tectonic changes that produced a deep Tasmanian 'gateway' between Australia and Antarctica were essentially complete by *c.* 30 Ma (Stickley *op. cit.*), and hence somewhat later than originally envisaged by McGowran *et al.* (1997).

With the opening of the Tasmanian Gateway, the oceanic circuit around the Australian continent was complete. At that time the Australian continent lay well south of its present position, with the region north of Australia lacking the flow constrictions presently imposed by the Indonesian Arc and associated terrains. With the opening of the Southern Ocean, Australia essentially represented an island, setting up a circulation forced by Godfrey's (1989) "Island Rule", which describes a circulation pattern forced by wind stress (Sverdrup circulation) setting up variations in steric height. With an open ocean north of Australia and the existence of the Tasmanian Gateway, tropical water, in part sourced from the Pacific, could now flow along the western margins of the continent, continue into the Bight, and return back into the Pacific. Hence, we see the first palaeogeographic setting for a Leeuwin Current type 'circulation' that bears resemblance to what is seen today, but one which is neither related to the temperature and salinity differences that are of fundamental importance to the dynamics of the present Leeuwin Currrent (Godfrey & Weaver 1997), nor does justice to the complexity of the flow-paths, that are now recognised in contributing to current dynamics (Domingues *et al.* 2007).

The Western Australian fossil record gives some suggestion that a SST pattern somewhat resembling that of today was in place by the Paleogene-Neogene transition. Inner shelf limestones of the Middle Miocene Poivre Formation of Barrow Island (McNamara & Kendrick 1994) feature diverse echinoid and molluscan assemblages, each with a strong tropical component. No comparable faunas are known from either the Perth or Bremer Basins but the Colville Sandstone of the marginal Eucla Basin (equivalent to the Nullarbor Limestone (Lowry 1968, 1970)) provides comparative evidence from the south coast for that time.

The mollusc assemblage from the Poivre Formation (71 spp.) is strongly tropical in character with notable representations of tellinoid and venerid bivalves and cerithioidean, strombid, cypraeid and conid gastropods. Elements in common with the Eucla Basin Middle Miocene (Colville Sandstone, Nullarbor Limestone) are few and apparently limited to the Tethyan relictual genus *Campanile*, the Australian endemic *Zoila*, and the species *Terebellum terebellum* (Linneaeus). The last mentioned species, which is extant, occurs in the Middle Miocene Nullabor Limestone, and the Miocene of Kerala, Java and Saipan (McNamara & Kendrick 1994).

This comparison of Middle Miocene echinoids and molluscs from Barrow Island and the Eucla Basin recognises a weak tropical component in the southern Australian assemblages, consistent with a remote, but only diffuse and sporadic proto-Leeuwin Current, capable of exerting no more than a slight influence on the faunal composition of inshore waters at that time. McGowran *et al.* (1997) however, argue for strong Leeuwin Current activity coincident with the Early–Middle Miocene boundary (*c.* 18–16 Ma). They place this event into a global sea level high context, in which a rising trend from the Late Oligocene to the latest Early Miocene is replaced by lowering sea levels in the Late Miocene. Coincident with the 'high-stand' of these events are globally warm SSTs, and the authors envisage a strong Leeuwin Current embedded within the global events.

The Indonesian Throughflow

Given the contribution that the Indonesian Throughflow makes to the source region of the Leeuwin Current, understanding the terrain restrictions and bathymetric controls north of Australia that presently direct the throughflow from the Pacific into the Indian Ocean, is of fundamental importance. An overview of the geological evidence points to the Indonesian Gateway being a feature with a long history (*e.g.*, Nishimura & Suparka 1997; Nishimura 2002; Gaina & Müller 2007). However, it now seems likely that it began to close by the Early Miocene, as indicated by deep water exchange stable isotope signatures between the two oceans (summary in Kuhnt *et al.* 2004). Subsequent restriction events on surface and intermediate water exchange will have occurred during the ensuing intervals of the Miocene to Pleistocene, but the evidence for such events is ambiguous and poorly constrained (Kuhnt *et al.* 2004).

Cane & Molnar (2001) claim that the Indonesian Gateway took on an expression resembling its present form during the last 3–4 myrs. In their view, the development of the geological-relief-bathymetric constraints offered by the tectonic re-organisation did not impact only on the details of the geography of the throughflow, possibly leading to a general cooling of the Indian Ocean (*cf.* Gordon *et al.* 2003, who advocate cooling due to monsoonal controls), but also may have led to changes in throughflow sources. Cane & Molnar (2001) envisage that at present much of the water constituting the Indonesian Throughflow is sourced from the North Pacific. Warm southern Pacific sourced water presently flows westward along the Equator in the Southern Equatorial Current. On reaching the island of Halmahera, it becomes part of the North Equatorial Counter Current and flows eastward. Cane & Molnar (*op. cit.*) propose that with New Guinea further south and with Halmahera being a smaller island, the warmer water from the South Pacific would have passed into the Indian Ocean rather than be involved in its present eastward transport path. However, recent particle track modelling reveals that the equatorial Pacific is also a source of Leeuwin Current water (Domingues *et al.* 2007). Nevertheless, the presently available views suggest that it has only been for the last few million years (essentially the Pliocene, 5–1.8 Ma) that a terrain arrangement north of Australia existed which imposed an exchange pattern between the Pacific and Indian Ocean resembling that of today. For a 'full' Leeuwin Current to have existed at that time, in addition to a restricted gateway, the temperature and salinity structure requirements over the Western Pacific Warm Pool and adjacent Indian Ocean would also have had to be met to provide the Indian Ocean and Pacific Ocean sources required (Godfrey & Weaver 1991; Domingues *et al.* 2007). In addition, a trade wind regime in the Pacific Ocean was necessary to contribute to the set-up of sea level in the western equatorial Pacific. Sato *et al.* (2008) present evidence that point to oceanographic conditions associated with the Indonesian Throughflow, similar to those of today, were established around 3–4 Ma, and that the Western Pacific Warm Water Pool had essentially taken on its modern form by that time.

The fauna of the early Late Pliocene Roe Calcarenite (*c.* 3–4 Ma (Beu & Darragh 2001; Kendrick unpublished data; Ludbrook 1978)) point to the existence of a strong Leeuwin Current at that time. The Roe Calcarenite is exceptional in the Australian Tertiary for its high species diversity and faunal composition. Its substantial warm-water component combines taxa descended from locally established Miocene lineages with others likely to be Late Pliocene immigrants from extraneous tropical or subtropical waters, consistent with a significant Leeuwin Current presence along the southern coast of Western Australia at the time of deposition.

The appearance in the early Late Pliocene of the Eucla Basin of a substantial, immigrant, warm-water faunal surge along the southern coast of Western Australia, presumably derived from an assertive Leeuwin Current, may bear some relationship to the timing of geological events in the Indonesian region (Cane & Molnar 2001), leading to the genesis of a distinct Leeuwin Current with controlling processes and dynamics akin to those at present. However, these inferences need to be placed within a more general context that recognises that the Middle Pliocene was a time during which mean global temperatures were substantially warmer than present (*e.g.*, Haywood *et al.* 2000) and with CO_2 levels higher than pre-industrial values (Raymo *et al.* 1996). Hence climatic factors also may have played a substantial role in the amplification of the current. The climatic effect suggested for current activity during the mid-Pliocene is a harbinger of the first-order control on the Leeuwin

Current, to be firmly established during Pleistocene times and continuing today.

Leeuwin Current activity over orbital time scales – the last *c.* 2 million Years

Once the terrain arrangement north of Australia resembled that of the present, the details of global climate dynamics became the sole drivers of Leeuwin Current events. Over the time scales of the last *c.* three million years, the Earth attained a full expression of the present ice age. Of special relevance is that during the last 1.75 myrs, the SST regime of the Western Pacific Warm Pool has been relatively stable (Garidel-Thoron *et al.* 2005), providing Leeuwin Current controls that may have been not dissimilar from those operating over Late Quaternary time-scales. It has now been firmly established that the Milankovitch mechanism provides the commonly termed "tuning fork" of global climates for this time. The dominant orbital periodicities operating in the Milankovitch mechanism centre on ~ 100 kyrs (eccentricity); 40 kyrs (obliquity-tilt); and 23kyrs and 19 kyrs (precession). Evidence for the operation of these mechanisms is given by the overwhelming weight of palaeoenvironmental studies and climate theory and modelling that now exists (*e.g.*, Lea 2004; Ruddiman 2007; Saltzman 2002; IPCC 2007). The Earth system responds to these changes by adjustments in ocean-ice volume distributions and internal arrangements of the global climate system with concomitant impacts on land-atmosphere-ocean characteristics and dynamics. Milankovitch insolation variations can lead to a direct response in ocean temperature (*e.g.*, Liu *et al.* 2003), which is an important driving control of the Leeuwin Current (Godfrey & Weaver 1997).

An insight into the likely impact of these variations can be obtained from idealised experiments using coupled ocean-atmosphere general circulation models. An example of this approach is the application of the Fast Ocean Atmosphere Model (FOAM), with variation in tilt and precession changes (see Wyrwoll *et al.* 2007 for details of the experiments). FOAM is a fully coupled ocean-atmosphere model without flux adjustment. The atmosphere component of FOAM is a fully parallel version of the NCAR CCM2, in which the atmospheric physics are replaced by those of CCM3 (Jacob 1997). The atmosphere component has R15 resolution (equivalent to grid spacing of about 7.5° longitude and 4° latitude). The ocean component was developed following the Geophysical Fluid Dynamics Laboratory Modular Ocean Model (GFDL MOM) with a resolution of 1.4° latitude and 2.8° longitude, 32 levels.

The results of the experiments show that both tilt and precession exert a significant control on SSTs, the surface wind field and precipitation patterns on the wider region that provides the setting for Leeuwin Current activity (Figure 1). Clearly the resolution of FOAM prevents a realistic exploration of what these changes may imply for Leeuwin Current activity. But the aim of the experiments was to draw attention to the likely controls that orbital changes may provide. A consideration of the possibility of a more direct Milankovitch forcing of the Leeuwin Current is more relevant to interglacial stages when the accompanying global boundary conditions are less complex. Liu *et al.* (2003) provide an example of the insight model studies offer when considering the ocean response to orbital forcing during an interglacial period.

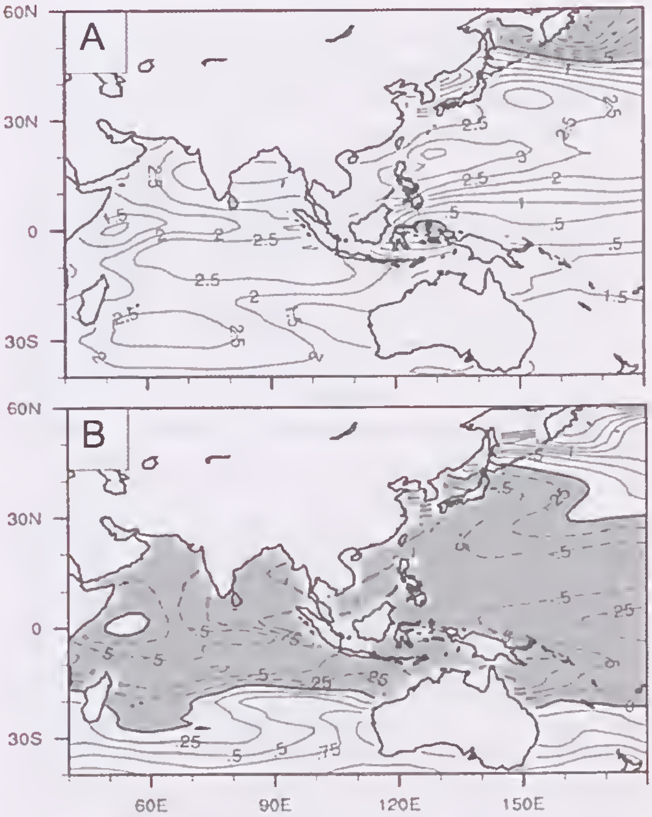


Figure 1. JFM Sea Surface Temperature (°C) of: (a) averaged Perihelion effects showing the difference between Precession in the Southern Hemisphere and Precession in the Northern Hemisphere(PS – PN); (b) averaged Tilt effects showing the differences between Tilt High and Tilt Low (TH – TL) for FOAM experiment (see Wyrwoll *et al.* 2007 for details of these experiments).

For the last 1–2 million years, the onshore marine sequences of the Perth Basin provide good indications that Leeuwin Current activity has varied significantly in that time. There, the Ascot Formation represents the Pliocene – Pleistocene transition. The predominant lithology is that of a grey, siliciclastic, mostly unlithified, richly fossiliferous arenite: subordinate carbonate is a feature of the older, more easterly member, for which diagnostic fossils include the bivalve *Cucullaea* and the pelagic janthinid gastropod *Hartungia*, both also present in the Roe Calcarenite. The Early Pleistocene younger member of the Ascot Formation records the initial appearance of the genus *Pecten* Müller in southern Australia, probably from a Mediterranean – Atlantic source via South Africa and the Antarctic Circumpolar Current (Beu & Darragh 2001; Beu 2006). Being entirely subsurface, no contact between the older and younger members of the Ascot Formation has as yet been observed, nor has superposition. In view of their consistent faunal discrepancies, any contact, if and where present, is likely to be unconformable, as envisaged by Beu & Darragh (2001, Figure 6).

Mollusc assemblages of the Ascot Formation are extensive but largely unrecorded beyond the limited listing of taxa in Kendrick *et al.* (1991) but, compared with that of the Roe Calcarenite, are clearly younger, include a distinct endemic element and are deficient, even devoid of, unambiguously warm-water taxa. This is true in particular for the younger Early Pleistocene Member. The formation as a whole signifies a regressive-cooling trend for the terminal Pliocene-Early Pleistocene, which was probably operative since the ending of Roe Calcarenite time.

In overview, the later and terminal Pliocene and entire early Pleistocene in southern Western Australia presents a picture of progressive oceanic cooling and regression, with the associated fossil record devoid of any recognisable warm-water component comparable with that so characteristic of the Roe Calcarenite. Throughout this interval no evidence can be recognised for the presence of the Leeuwin Current on regional scales in southwestern Australia.

A notable event that occurred in the coastal-marine sequences of the Perth Basin is the change from siliciclastic deposition (represented by the Ascot Formation) to the carbonate style of deposition of the Tamala Limestone (Kendrick *et al.* 1991). The change to a carbonate style of sedimentation may be interpreted as being the direct result of higher rates of carbonate productivity, but other explanations may also apply (see Kendrick *et al. op. cit.*). However, the evidence for higher sea surface temperatures during the Middle Pleistocene, as compared to those during the time of deposition of the Ascot Formation, is indicated by the molluscan faunas, which signify greater tropical and subtropical affinities than evident in the Ascot Formation. The weak representation of tropical and sub-tropical elements in the mollusc fauna of the older Plio-Pleistocene units of the Perth Basin suggests that the Leeuwin Current was then either of lesser importance than during the Middle Pleistocene, or not active. Unfortunately, at this stage we have no absolute age control of these events.

There is now evidence that there was an increase in ΔSST gradient of ~ 3.5 to ~ 5°C between the eastern and western equatorial Pacific during the interval, 1.2–0.8 myrs ago (Garidel-Thoron *et al.* 2005). The suggestion is that this would have strengthened the Walker Circulation and led to a shift from a more El Niño state to La Niña conditions. Variations in Leeuwin Current strength to El Niño-Southern Oscillation (ENSO) variations are well known, with strong and weak Leeuwin Current flow characterising La Niña and El Niño states, respectively (Pearce & Philips 1988; Li & Clarke 2004). The shift from a more dominant El Niño state to La Niña conditions during the period 1.2–0.8 myrs ago may be a factor worth considering in accounting for the Ascot Formation/Tamala Limestone contrasting evidence of Leeuwin Current activity.

Of the interglacial sea level events that are evident in the Middle and Late Pleistocene marine record of the western margin of Australia (Kendrick *et al.* 1991; Bastian 1996), it is only for the Last Interglacial centred on 125 Ka (Marine Isotope Substage (MIS) 5e) that reliable numerical dates are available. Previous to the present sea level high stand, the Last Interglacial was the last time that a comparable sea level high to that of the last *c.* 6 000 years has occurred. The Last Interglacial was a time during which global climates were generally similar to today but with global temperatures higher than at present (Kukla *et al.* 2002; North Greenland Ice Core Project Members 2004).

A stronger than present Leeuwin Current – the significance of the Last Interglacial

Western Australia presents a relatively stable continental margin in a far-field location, with a comprehensive Last Interglacial stratigraphic record readily lending itself to the reconstruction of sea level events. The recognised events attest to a Last Interglacial sea level high stand which is pervasive in the coastal geomorphology of much of Western Australia. The high stand produced a sea level of about +4 m and persisted from between 128±1 Ka and 116±1 Ka (Zhu *et al.*1993; Eisenhauer *et al.*1993; Stirling *et al.* 1995, 1998). The likelihood that during this time two sea level high events occurred has been an issue of discussion for many years (Marshall & Thom 1976; Kendrick *et al.* 1991) and is now attracting renewed interest (Andrews *et al.* 2007; Hearty *et al.* 2007). Greenstein *et al.* (2005) have recently proposed the likelihood of evidence for two Last Interglacial sea level high stands in the Exmouth Gulf, but the dating in support of this claim remains to be completed.

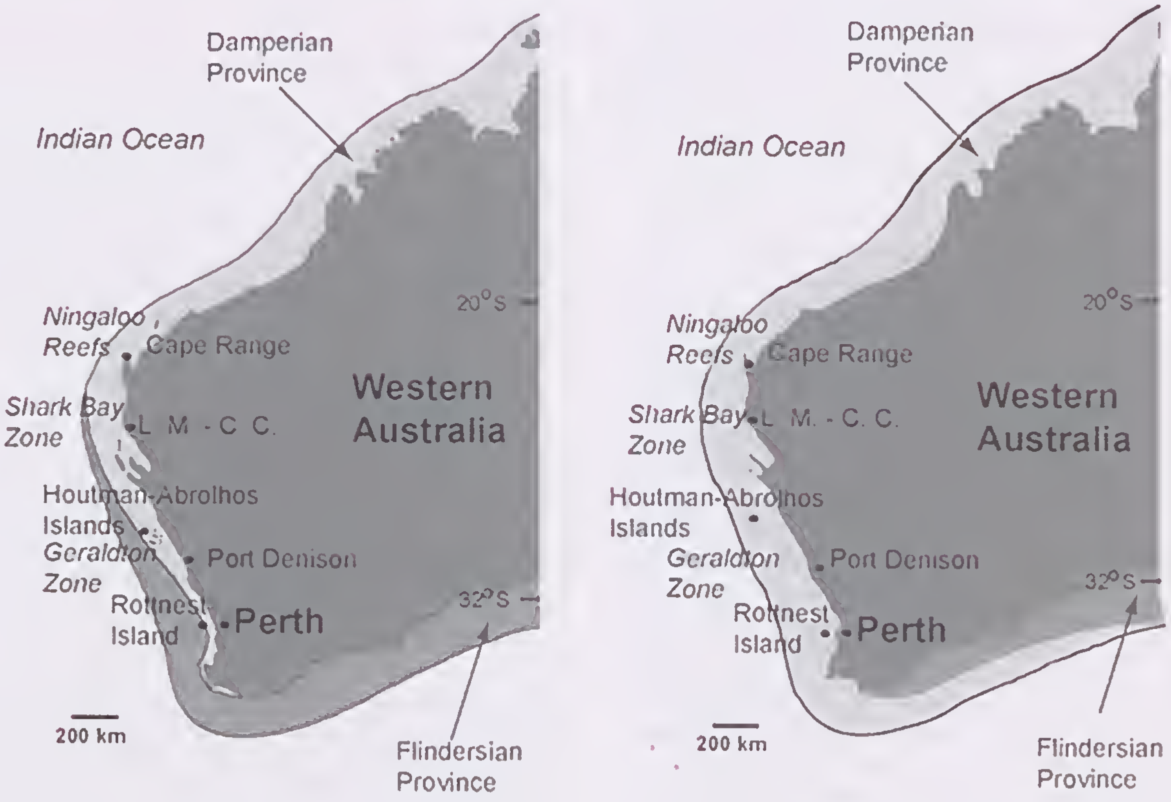
The Last Interglacial is of fundamental importance in demonstrating that the Leeuwin Current influences the geographic reach of extensive coral reef development along the Western Australian coast. Because of their high initial uranium content, corals are well suited for ^{234}U – ^{230}Th dating, and an impressive suite of dates is now available for many sites along the Western Australian coast (Szabo 1979; Veeh *et al.* 1979; Kendrick *et al.* 1991; Zhu *et al.* 1993; Stirling *et al.* 1995, 1998; Eisenhauer *et al.* 1996; McCulloch & Mortimer 2008). In this respect the Last Interglacial differs fundamentally from the earlier interglacials present in the Quaternary sea level record of the southern part of Western Australia that essentially lack coral reef-building events.

Hermatypic corals of the reef-building genus *Acropora* are prominent in suitable shallow water habitats of Australian tropical seas, and in Western Australia forming elaborate coral "gardens", which today extend south to the Houtman Abrolhos (Veron & Marsh 1988). In addition, three species of *Acropora* have been found living near Jurien Bay and one has become established recently at Rottnest Island, the latter situated at the extreme latitudinal limit of *Acropora* survival (Marsh 1993). This distribution differs fundamentally from that of the Last Interglacial, during which fringing coral reef development extended well south of the Houtman Abrolhos. The prominent reef exposed at Fairbridge Bluff on Rottnest Island (Szabo 1979; Playford 1988), rich in *Acropora* (tabular and stag-horn forms) and other hermatypic corals, was among the earliest recognised evidence widely seen as attesting to a southward extension of tropical reef assemblages during the Last Interglacial.

A tropical coral fauna, similarly attributed to the Last Interglacial, occurs at Fremantle with evidence of a coral-rich limestone bar, once located between Rous Head and Arthur's Head and removed during construction of the Fremantle inner harbour in 1892–1897, and elsewhere as far south as Augusta. There, a richly fossiliferous, emergent deposit is exposed along the eastern side of the entrance channel to Hardy Inlet and continues into an adjacent quarry. Associated with *Acropora* specimens from here are the tropical pearl oyster *Pinctada fucata* and the gastropod *Strombus (Euprotomus) vomer*. Further east at Cheyne Bay a shelly, coralline aggregate, well above present sea level is cemented to a crystalline basement and forming a small promontory about 0.5 km north of the mouth of the Eyre River, at the western end of Cheyne Bay. Coralline material from this deposit includes both *Acropora* and a specimen of the tropical genus *Cyphastrea*, the latter not known living south of Cockburn Sound (L.M. Marsh *pers. com.*). At the Pallinup River mouth a specimen of *Acropora* has been obtained from a lithified shore deposit lying at about 3 m above low water mark. This is currently the most marginal record for the genus known from southern Western Australia.

Last Interglacial emergent reefs along the coast of Western Australia expose coral assemblages that are remarkably well preserved, allowing for a great number of taxa to be identified with a degree of certainty that compares closely with modern material. The Last Interglacial reefs exposed from Rottnest Island to North West Cape span some 12 degrees of latitude. Today the region comprises the Western Overlap Zone between the tropical Dampierian and temperate Flindersian provinces (Wilson & Gillett 1980). Greenstein & Pandolfi (2008) censussed Late Pleistocene reef coral communities preserved at five separate localities between Rottnest Island and North West Cape and compared their data with those published for adjacent modern reefs (Figure 2). Between-community (beta) diversity was markedly different between times owing to the extended geographic ranges of tropical-adapted taxa during the Last Interglacial compared to today (Figure 3).

While the palaeoecological evidence is clearly consistent with an enhanced Leeuwin Current during the Last Interglacial, geochemical data seem to question this claim. Corals through their trace element composition (Sr/Ca, Mg/Ca and U/Ca) provide quantitative estimates of sea surface temperatures (see Bradley 1999; Cole 2005), including seasonal differences. Using Sr/Ca ratios from the Last Interglacial at Ningaloo, McCulloch and Esat (2000) obtained summer maximum temperatures ranging from 26°C to 28°C and winter minima ranging from 23°C to 20°C with an annual mean temperature of 24°C. These SSTs estimates are slightly cooler than present and the authors recognise that their results sit uncomfortably with the palaeoecological evidence indicative of a stronger Leeuwin Current during the Last Interglacial. They advocate the view that this apparent paradox may be resolved by advocating increased summer maximum temperatures rather than winter minimum SSTs,



Modern

Late Pleistocene

Figure 2. Modern and Pleistocene localities used for comparative study by Greenstein & Pandolfi (2008) and their disposition with respect to the Dampierian and Flindersian provinces today and during Late Pleistocene time. Disposition of modern provinces after Wilson & Gillett (1980); exact location of the "overlap zone" during Late Pleistocene time is unknown. Modern reef zones after Veron & Marsh (1988); L. M. – C. C. = Lake Macleod – Cape Cuvier.

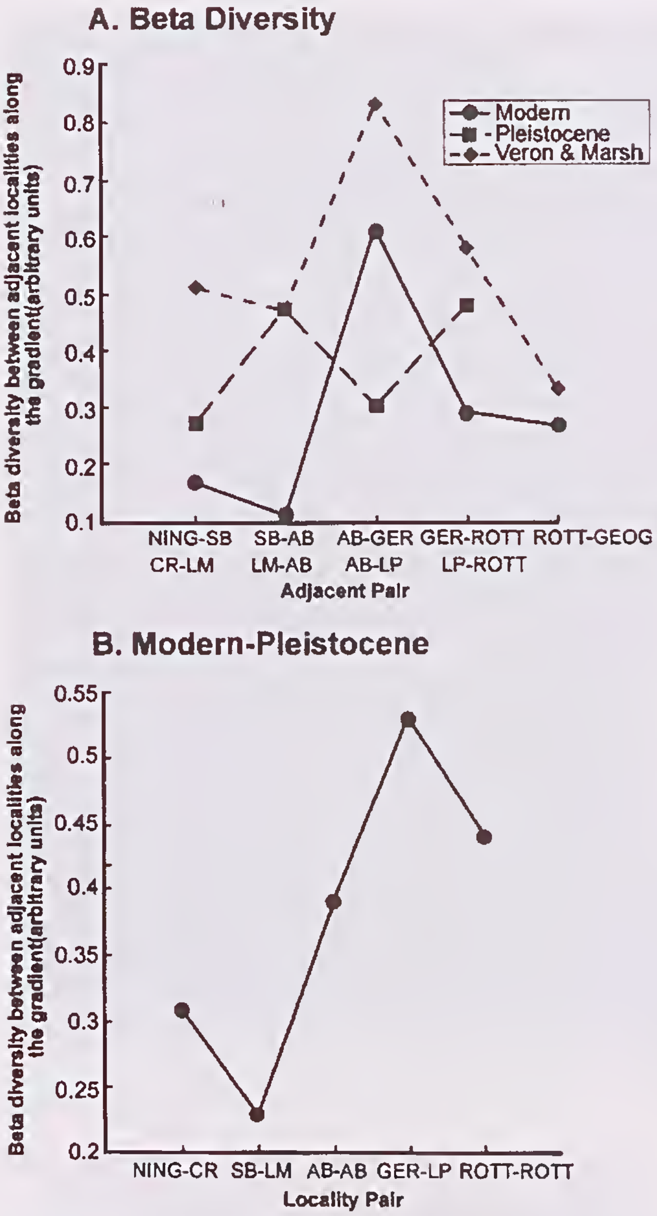


Figure 3. Analysis of beta diversity presented by Greenstein & Pandolfi (2008). A) Beta diversity computed between adjacent localities for modern (full data set of Veron & Marsh 1988; culled data set using only modern taxa that are also represented in Pleistocene reefs) and Pleistocene reef coral communities. A comparison to an additional modern locality south of the study area (Geographe Bay) indicates that lower beta turnover resumes within the Flindersian Province. For modern reefs NING = Ningaloo, SB = Shark Bay, AB = Abrolhos, GER = Geraldton, ROTT = Rottnest Island, GEOG = Geographe Bay. For fossil reefs CR = Cape Range, LM = Lake Macleod-Cape Cuvier, AB = Abrolhos, LP = Leander Point, ROTT = Rottnest Island. Gradient beta diversity and additivity are indicated in upper left. B) Beta diversity between modern and Pleistocene localities present at each latitude, abbreviations as in A, above.

suggesting that during Last Interglacial summers the Leeuwin Current was more intense and delivered a larger volume of warm water to the southern coast of Western Australia. They draw attention to a modern analogue, the high latitude reefs of southern Japan, where coral calcification occurs mainly in the summer months in response to the warm Kuroshio Current. Additionally, McCulloch & Esat (2000) were unable to provide a reliable age for the coral analysed but associated it with an assemblage dated at 128–122 Ka.

There are other claims of varying SSTs during the Last Interglacial. Wells & Wells (1994) in their reconstruction of the ocean circulation off Western Australia indicate a significant reduction in SSTs at 130 Ka. They suggest that at 120 kyrs, winter SSTs off the North West Cape were 3°C higher than at present, with a 'pool' of colder water to the west. In adopting this inference, it needs to be recognised that the SSTs of Wells and Wells tend to underestimate SST (Barrows *et al.* 2000). On the basis of ^{234}U – ^{230}Th ages, Stirling *et al.* (1998) concluded that coral growth associated with a Last Interglacial sea level high stand along the Western Australia margin spans the period *c.* 128–121 Ka, seeing this as a period of reef growth after which reef growth was arrested due to lower SSTs. They considered two alternate, though not mutually exclusive possibilities: (i) reef termination may have been related to a sudden switching off of the Leeuwin Current at *c.*121 Ka, a consequence of global climate events; (ii) the absence of coral reefs may simply be due to a more oscillating sea level history after *c.* 121 Ka, preventing reef growth. However, in the Houtman Abrolhos a coral reef fringe is preserved in a sheltered location in the Wallabi Group and has been dated to 117–116 Ka (Zhu *et al.* 1993). Furthermore, in cores from the Ningaloo reef barrier there is clear evidence of coral growth until *c.* 115±2 Ka (Collins *et al.* 2003). At least for these areas, the indications are that reef growth may not have been constrained by lower SSTs during the later part of the Last Interglacial.

In summary, it is clear that our understanding of Last Interglacial events, both in terms of sea level changes and likely differences in SSTs, is incomplete. Nevertheless it can be confidently concluded that the palaeoecological data from southwestern Australia indicate a stronger than present Leeuwin Current during at least part of the Last Interglacial. If we follow the argument of Stirling *et al.* (1998) that coral growth (at least for the region south of the Houtman Abrolhos) spans the period *c.* 128–121 Ka, and that subsequently reef growth was arrested due to lower sea surface temperatures, recent general circulation experiments allow an exploration of the mechanisms by which this occurred.

Wyrwoll &Valdes (2003) undertook a sensitivity experiment to establish the response of the northwest Australian monsoon to a precession driven, high insolation event that characterised the low latitudes of the Southern Hemisphere at 115 Ka. The sensitivity experiment used the high resolution Hadley Center climate model – HadAM3 version of the U.K. Meteorological Office's Unified Model (Pope *et al.* 2000). One result of the experiment showed a significant increase in lower tropospheric southerly winds along the coast of Western Australia during March (Figure 4). In light of the fact that the Leeuwin Current is controlled by the balance between a southward pressure gradient force and a northward wind stress, this could relate to reduced Leeuwin Current activity during the later part of the Last Interglacial. However, why a stronger Leeuwin Current existed at other times during the Last Interglacial, remains an open question.

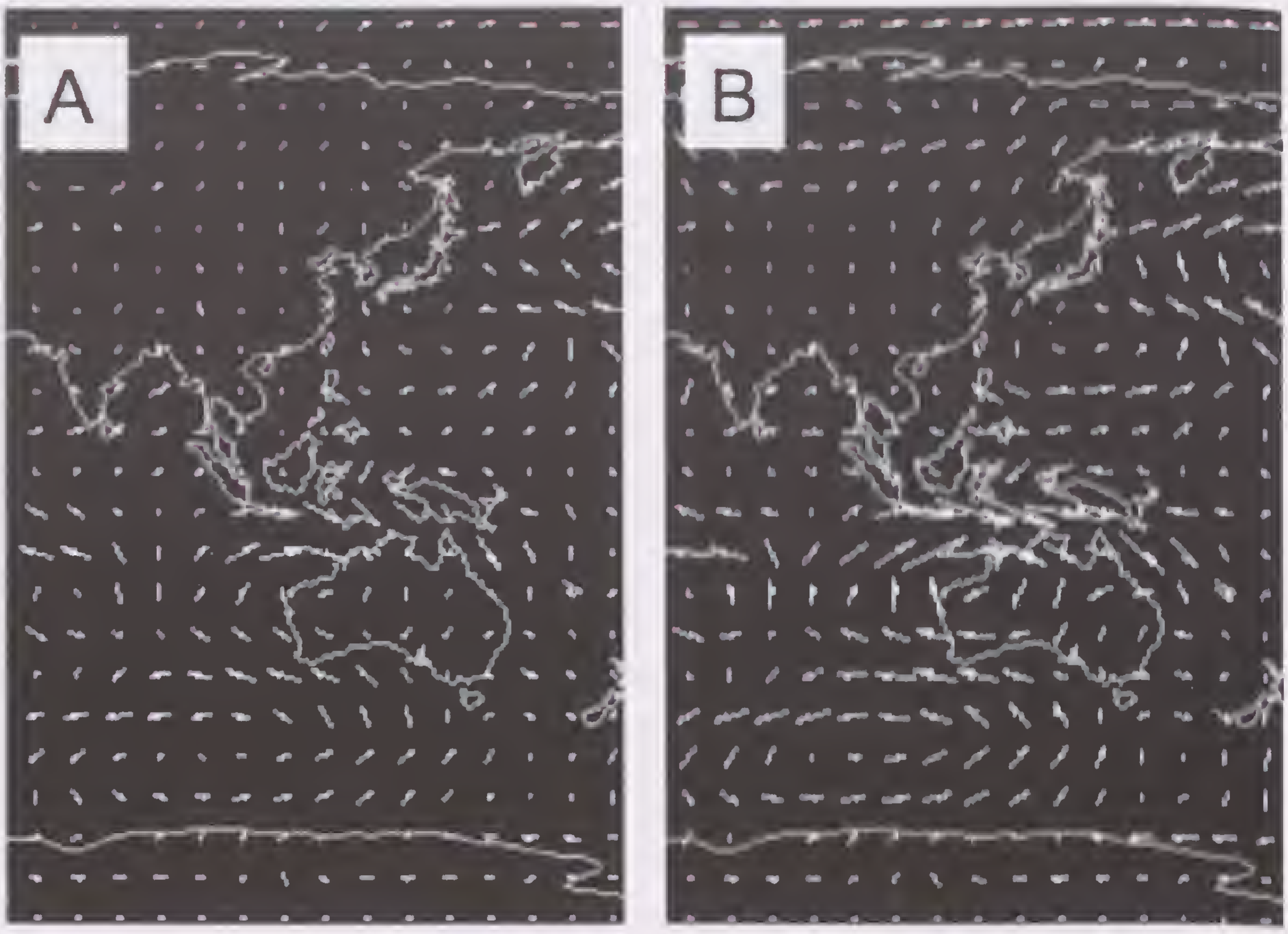


Figure 4. HadAM3 model results for 115 Ka (March) indicating increased strength (with respect to present) of southerly winds along the western Australian margin: (a) Surface winds; (b) Winds at 850 hPa.

Sea level and Leeuwin Current events during the Late Pleistocene

Figure 5 provides a detailed sea level history from the Last Interglacial to the present. It is clear that for much of this time sea level was lower than present. Consequently, only evidence recovered from ocean cores exists, and even that is very limited. Rivers *et al.* (2007) suggested that there is evidence during Marine Isotope Stage 3 (MIS 3) (*c.* 30–60 Ka) for the presence of a warm-water current in the Great Australian Bight, and relate this to the Leeuwin Current. Takahashi (2000) recognises a weakening of the Leeuwin Current during the end of MIS 3.

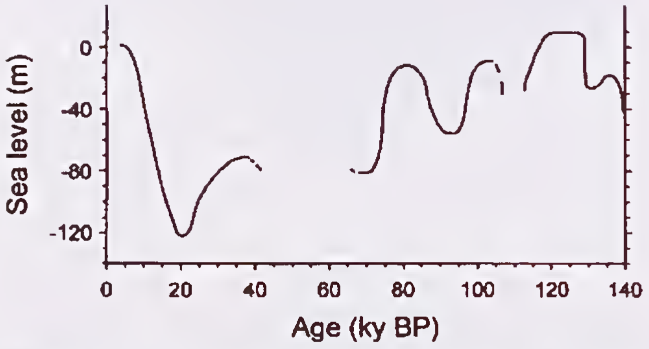


Figure 5. Sea level history for the last *c.* 140 000 years (after Cutler *et al.* 2003).

The Last Glacial Maximum

Because it marks the nadir of the last glacial, the Last Glacial Maximum (LGM), *c.* 21 Ka, provides a profound contrast to the Last Interglacial, prompting interest in the status of the Leeuwin Current at that time. Massive global-scale reorganisation of both atmospheric and oceanic circulations characterised the LGM, with sea levels some 130 m lower than at present. With the lowering of sea level, a massive extension of the land area of Western Australia occurred and with it, major changes in the Indonesian Archipelago (Figure 6). In Western Australia, land extensions were most dramatic over the northwestern region, while further south they were less defined, notably in the North West Cape region – where the shelf is at its narrowest. How these changes in geography may have affected Leeuwin Current activity remains to be explored but given the partial dependence of the Leeuwin Current on the Indonesian Throughflow (Domingues *et al.* 2007) more constricted passages with the low sea levels of the LGM should have reduced its strength. At present there are differing views

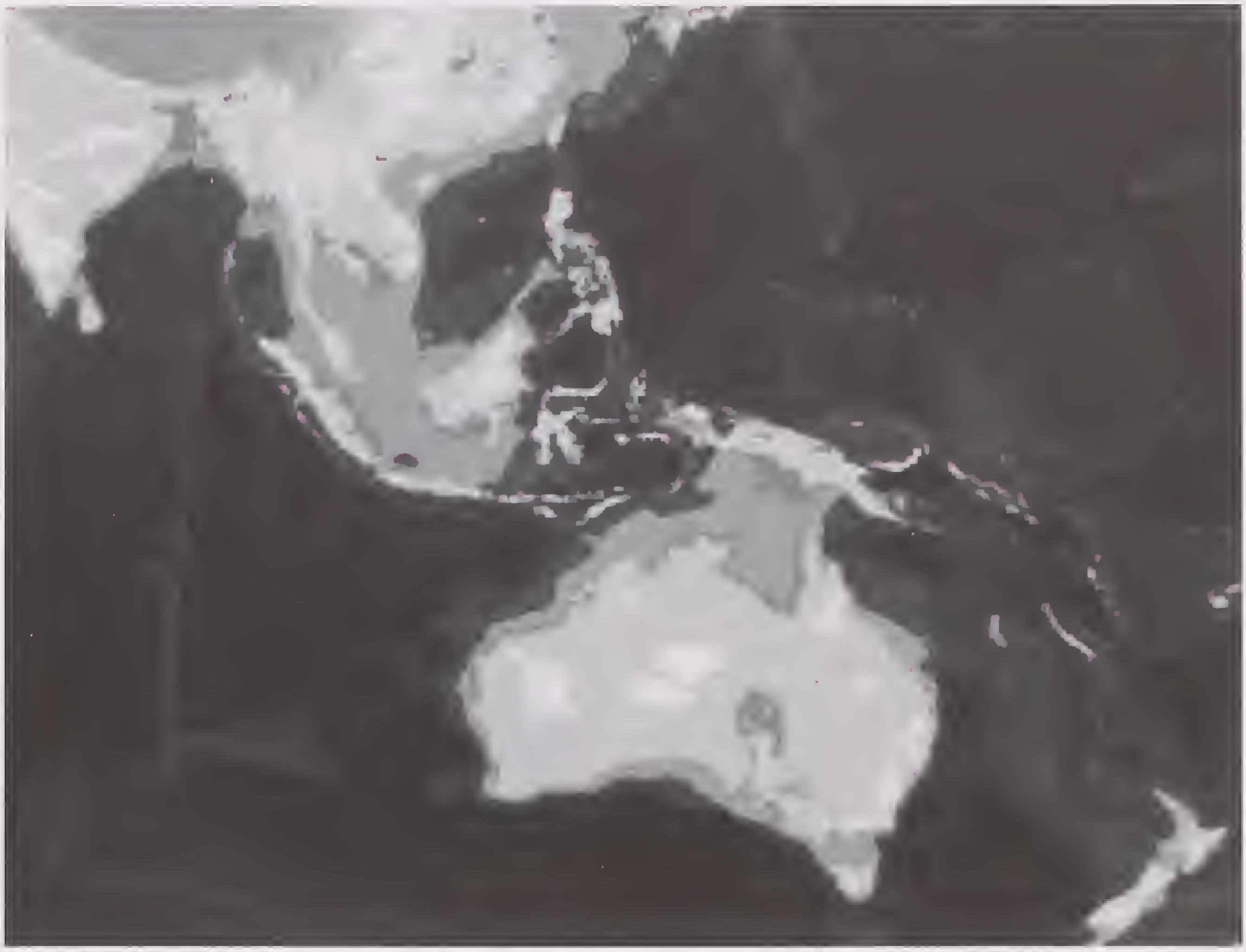


Figure 6. Land extension over the wider Australian-Asian region at the Last Glacial Maximum. Sea level at that time was ~130 m lower than present.

on the state of the Leeuwin Current during the LGM. An overview of the eastern Indian Ocean circulation and more specifically Leeuwin Current activity during this time is provided by Wells & Wells (1994). They conclude that a significant change in SSTs occurred at the time, amounting to a maximum winter (summer) 6°C (7°C) decrease in SSTs in the region of North West Cape and attribute these changes to a more active West Australian Current at that time, in the absence of the Leeuwin Current. Results of work in the Great Australian Bight (Rivers *et al.* 2007) concur with the view that, during much of Marine Isotope Stage 2 (25–11.4 kyrs), the Leeuwin Current was weak or absent – a view also supported by Takahashi (2000).

A wider evaluation of SSTs at the LGM by Barrows & Juggins (2005) suggests that the Leeuwin Current was still active at that time, even though tropical cooling of up to 4.1°C was proposed. These authors recognise an equatorward displacement of isotherms in higher latitudes, indicating colder water transport along the west coast of Australia into low latitudes. According to Barrows & Juggins (*op. cit.*), at the LGM the greatest cooling of 3–4°C occurred between 17–22°S, indicating a stronger West Australian Current at that time. The lower SST estimates of Barrows & Juggins are significantly lower than those of Wells & Wells, who advocated reductions of up to 7°C for this region. Of great significance is their accompanying claim of an active Leeuwin Current at the LGM, albeit transporting cooler water than today (Barrows & Juggins 2005). They see an active Leeuwin Current as being the reason for an apparent absence of an eastern boundary upwelling regime. In support of their view the authors cite Veeh *et al.* (2000), who found little evidence for increased upwelling along the coast of Western Australia during the LGM and had also drawn attention to the likelihood that the Leeuwin Current was active at that time.

Latest Pleistocene

Investigations of chemically- and biologically-mediated precipitation of carbonate materials have been claimed to provide indications of the onset of the Leeuwin Current after a supposed absence during the LGM. James *et al.* (2004) suggest that ooid formation on the northwest shelf required higher salinity than at present and gave ^{14}C ages of 15.4–12.7 Ka for ooid formation. In their interpretations, the salinity levels required for ooid formation are thought to indicate the absence of the Leeuwin Current at that time. In support they cite the work of Gingele *et al.* (2001 a & b) who, on the basis of clay mineralogy, suggest that the Leeuwin Current onset occurred at *c.* 12 Ka, claims that need to be reconciled with the views of Barrows & Juggins (2005) and Veeh *et al.* (2000) of an active Leeuwin Current at the LGM.

While the issue of a possible active/inactive Leeuwin Current at the LGM (or the degree to which this may have been the case) cannot be resolved at present, there can be no doubt that the Leeuwin Current was fully established during the final few millennia of the Pleistocene. Drilling of the Houtman Abrolhos coral reef build-up has shown that by *c.* 10 Ka, a coral reef complex was firmly established (Collins *et al.* 1993; Wyrwoll *et al.* 2006). An intriguing aspect of the seismic stratigraphy obtained from the Houtman Abrolhos is the existence of a reflector (recognised in the Easter Group) at a depth of ~ 40 m. It seems likely that this 'reflector' indicates the 'surface' on which late Pleistocene reef colonisation took place. Reef accumulation rates established for the interval *c.* 10 Ka to present (~ 6 m/kyrs) would require the onset of reef growth to date to *c.* 13 Ka, necessitating a fully established Leeuwin Current prior to that time in order to allow coral colonisation.

The Leeuwin Current over Holocene and historical time scales and associated ENSO variations

Records of Leeuwin Current activity during the last few thousand years are obtained by analyses of the $\delta^{18}O$ composition of coral colony skeletons. Massive corals provide the best-known avenue for developing annually resolved climate proxy records throughout the tropical oceans (*e.g.*, Cole 1996; Dunbar 1996; Gagan *et al.* 2000). As they grow, these corals record, in the chemical composition of their aragonitic skeletons, information about the physical and chemical environment of the surrounding seawater. This attribute, combined with rapid growth rates (10–20 mm/year), their longevity (centuries to millennia) and the presence of annual bands (analogous to tree rings), means that they can yield high resolution (*e.g.*, monthly) records of past environmental change over hundreds of years, with a temporal resolution of +/- a few weeks. In order to absolutely resolve temperature vs. seawater composition effects on skeletal $\delta^{18}O$, it is necessary to use combined oxygen isotopic and Sr/Ca analysis. The recently developed technique for quantifying both SST and water composition (salinity) changes using combined tracers has proved extremely effective in both living and fossil corals (McCulloch *et al.* 1994, 1996, 1999; Gagan *et al.* 1998; Tudhope *et al.* 1998; Crowley *et al.* 1999; Ren *et al.* 2003).

An attempt to obtain an indication of Leeuwin Current activity over centennial timescales is provided by Kuhnert *et al.* (1999, 2000). In determining the oxygen isotope ($\delta^{18}O$) composition of cores from coral colonies of *Porites lutea* from both the Houtman Abrolhos and Ningaloo Reef, SST records were developed for the last 200 years and 116 years, respectively. A general trend identified from both sites was a long-term increase in SST amounting to 0.7°C/century for the Houtman Abrolhos and 1.5°C for Ningaloo Reef. The apparent increase in SSTs of 1.5°C is considered problematic and likely to be too high due to uncertainties in the $\delta^{18}O$-SST calibration. Regardless of this uncertainty, the coral record does suggest that the overall warming observed is not coupled to a change in the seasonality of the Leeuwin Current. Allan & Haylock (1993) had already recognised increases in SSTs off the northern and central-west region of Australia (also see Lough 2008), corroborating the trend identified in the coral record. More recently, Feng *et al.* (2005) point to an additional overall Indian Ocean warming of 0.6°C in the period, 1991–2000. Similarly, the continental shelf off Western Australia has seen an increase in SSTs of ~ 0.6°C over the past 50 years (Pearce & Feng 2007).

In the Ningaloo Reef coral record there are indications of short-lived decreases in SST related to volcanic eruptions (Kuhnert *et al.* 2000). The suggestion is of a 1°C SST decrease associated with the Pinatubo eruption (1991) and a possible signal associated with the Krakatau event (1883). In previous work Gagan & Chivas (1995) also identified the Pinatubo event in the stable isotope record of corals from the Ningaloo Reef. They were able to relate this to SST changes induced by the Pinatubo eruption in the Western Pacific Warm Pool (WPWP), some 2.5 years previously and transmitted to the Ningaloo region via the Leeuwin Current. These authors suggest that the eruption-induced cooling of the WPWP could have impacted on the duration (1991–1994) of a negative phase of the Southern Oscillation. It is clear from these data and wider considerations (Cane 2005) that some of the variability evident in Leeuwin Current activity can be attributed to volcanic events and underscores the sensitivity of the system to regional events operating over human time-scales.

As already noted, the importance of El Niño-Southern Oscillation (ENSO) in determining the strength of the Leeuwin Current is well established. However, the attempts to link the 200-year coral $\delta^{18}O$ proxy record of SSTs from the Houtman Abrolhos to possible variations in Leeuwin Current activity have met limited success, finding only a weak covariation between Leeuwin Current strength and coral $\delta^{18}O$ (Kuhnert *et al.* 1999). A periodicity of 3–5 years is evident in the coral record and some consideration has been given to the possibility that this may be indicative of ENSO events. But it is noteworthy that a similar periodicity is not evident in the Ningaloo Reef record, in which a 9 year periodicity in SSTs is dominant.

It is well known that ENSO events have a complex history when considered over long time scales (*e.g.*, Tudhope *et al.* 2001; Turney *et al.* 2004; Rein *et al.* 2005). Model results suggest that seasonal changes in insolation alone can result in changes in ENSO characteristics (Clement *et al.* 2000; Cane 2005). Rein *et al.* (*op. cit.*) provide a comprehensive appraisal of the record of ENSO events over the last 20 kyrs. They show that a phase of stronger El Niño activity started in Peru around 17 Ka. Very strong El Niño activity occurred during the early and late Holocene, especially during the second and third millennia B.P. El Niño events were weak before and during the beginning of the Younger Dryas, during the middle of the Holocene and during Medieval times. An earlier compilation by McGregor & Gagan (2004) drew on coral $\delta^{18}O$ records throughout the west Pacific to provide details of the variation of ENSO occurrence during the Holocene. They recognise 12 events/century for the period 7.6–7.1 Ka; 8 events/century for the period, 6.1–5.4 Ka; and 6 events/century at 6.5 Ka. During 2.5–1.7 Ka, the coral records indicate large and protracted $\delta^{18}O$ anomalies indicative of particularly severe El Niño events. They note specifically, that the 2.5 Ka Madang Papua New Guinea corals record a protracted 4-year El Niño, like the 1991–1994 event, but almost twice the amplitude of the 1997–1998 event (Tudhope *et al.*2001). In addition, they recognise that the 2 Ka Muschu Island (Papua New Guinea) coral $\delta^{18}O$ record shows a severe 7 year El Niño, longer than any recorded Holocene or modern event. This is supported by the findings of Woodroffe *et al.* (2003) who analysed a late Holocene coral record from Christmas Island (central Pacific) and found evidence for an extreme El Niño that was twice the amplitude of the 1997–1998 event. Significant variations are also evident in the more recent historical record (*e.g.*, Allan *et al.* 1996). Given the strong and generally accepted relationship between the strength of the Leeuwin Current and ENSO events, the now-established record of ENSO makes it clear that the Leeuwin Current must have shown marked variations over a range of time-scales. Such variability must have imprinted itself on the biota leading it to acquire a 'plasticity' that equipped it to accommodate ENSO variability or, alternatively, forcing marked changes in population size resulting in 'bottle-neck' effects (B. Knott, *pers. com.*). Observed 'plasticity' in the biota should inform ecological notions as to whether marine communities represent loose associations of component taxa that respond individually to environmental change, or more integrated associations that are predictable in space and time.

Some lessons for the future?

Forcing mechanisms

A challenge facing us is predicting the response of the Leeuwin Current to anticipated future greenhouse climate states and likely accompanying biotic changes. Since the trajectory of human induced climate change is forecast to continue into the foreseeable future (IPCC 2007), predicting the impact of climate change on the abundance and distribution of organisms has become increasingly urgent. The western margin of Australia provides no exception to this, with possible future changes in Leeuwin Current activity having potentially far-reaching implications for the marine biota. An early attempt at considering the likely response of the Leeuwin Current to global warming and the implications this carries for marine organisms was provided by Pattiaratchi & Buchan (1991). Their attempt at identifying the possibilities of changes in forcing mechanisms was greatly hampered by the limitations of global climate models at the time of study. These limitations were highlighted by their inability to establish the likelihood of possible ENSO changes under enhanced greenhouse conditions – a foremost consideration in any assessment of future Leeuwin Current activity. The restrictions imposed by model limitations were still evident by the time of Cane's (2005) review, and even today only guarded conclusions can be drawn from available simulations. The Fourth IPCC report (IPCC 2007) concludes that present model simulations still give no consistent indication of discernible changes in projected ENSO amplitude or frequency in the 21st century.

Biological response

Whatever models may ultimately predict about future climate states and their impact on Leeuwin Current activity it is clear that at the most general level, the Earth has experienced significant anthropogenic warming over the last *c.* 100 years. We know that 'warm Earth' periods evident in the global climate record have imprinted themselves on Leeuwin Current activity – as evidenced in Western Australia by the fossil assemblages preserved in the Roe Calcarenite and the Last Interglacial (MIS 5e) deposits. Given this evidence, it would seem sensible to turn to past 'warm Earth' events and use these as analogues to explore the nature of Leeuwin Current activity and the biological response under a future warm climate state. The use of 'geological analogues' to complement model climate predictions (*e.g.*, IPCC 2007) is not without potential pitfalls. One of the most challenging is that past 'warm' states were insolation driven, while future climates are a response to anthropogenic greenhouse forcing. Nevertheless, using past 'warm Earth' Leeuwin Current states may help to shed some light on the course of future events.

At the global-scale the Last Interglacial was warmer than the present interglacial, clearly evidenced by proxy palaeoclimate data-sets (Kukla *et al.* 2002) and reflected in higher than present sea levels (Stirling *et al.* 1998), indicating lower ice volumes. It was clearly a time of stronger than present Leeuwin Current activity, which had a profound impact on shallow marine ecosystems adjacent to coastal Western Australia. Many of the important components of these systems have been preserved as fossils and palaeoecological studies of these deposits allow us to begin to understand ecosystem responses to climate change over spatial and temporal scales unavailable to modern ecological studies. The results may then be used as a step towards understanding the likely responses of shallow marine communities to future global warming. The assumption underlying this approach is, of course, that in a future warmer Earth, Leeuwin Current activity will mirror past 'warm Earth' responses.

The results of recent work (Greenstein & Pandolfi 2008) predicting the response of coral taxa to future greenhouse induced Leeuwin Current changes, provides insight into the potential that this approach holds. Already, present climate change is resulting in noticeable range expansions of coral taxa in the Caribbean (Vargas-Ángel *et al.* 2003; Precht & Aronson 2004) and the Indo-Pacific (Marsh 1993) provinces. The genus *Acropora* was reported living for the first time from Rottnest Island by Marsh (1993), who attributed the presence of *A. youngei* to both increased temperature as well as lack of competition from macroalgae. Range expansions of individual coral taxa will likely continue as temperature increases over the next century. Greenstein & Pandolfi (2008) predict that certain acroporid and faviid corals would appear in regions south of the Houtman Abrolhos Islands in the future. Although such predicted geographic shifts of coral taxa will not mitigate ecological and economic losses resulting from localised mortality, range expansions of important contributors to tropical reef coral communities may allow them to persist in "temperature refugia" in the wake of future climate change.

Greenstein & Pandolfi (2008) also found that less faunal change occurred between fossil coral communities between North West Cape and Rottnest Island compared to the adjacent modern coral communities offshore. A similar decrease in beta diversity between communities may occur as tropical-adapted coral taxa expand their geographic ranges south along the coast of Western Australia in the future. This effect may be amplified by preferential survival of particular coral taxa (*e.g.*, Done 1999). Although the reasons for the correlation are controversial, the role of biodiversity in enhancing ecological stability has been demonstrated on small spatial and temporal scales (*e.g.*, McCann 2000; Naeem & Li 1997; McGrady-Steed *et al.* 1997). However, it remains to be demonstrated whether regional ecological stability and beta diversity are correlated. In summary, this recent comparative study of Pleistocene and modern corals in coastal Western Australia elucidates the likely impact of increasing Leewuin Current activity on coral faunas in the region. Additional work predicting the impact on coral community membership remains to be attempted.

Concluding discussion

A unique aspect of geological study of evidence for the Leeuwin Current is that it allows a distinction to be made between factors that affected the current over significantly different time scales. For example, the early history of the Leeuwin Current is characterised by changes that took place over time intervals quite beyond human experience. The interplay of tectonics (deepening of the Tasmanian Gateway followed by emplacement of today's Indonesian Archipelago) and ocean circulation took place over tens of millions of years, and established the initial foundation for "Leeuwin Current style" along the western margin of Australia. Whether prior to this, the evidence of warm sea surface temperatures should be ascribed to the existence of a "proto-Leeuwin Current" can be questioned. It may be more appropriate to relate the existence of the Leeuwin Current to its forcing mechanisms, and not simply claim its existence on the basis of elevated SSTs.

Once the Leeuwin Current *sensu stricto* was emplaced by these processes 2–3 million years ago, its geologic history comprised alternate waxing and waning in response to forcing mechanisms related to climate rather than tectonics. Although shorter term climatic changes certainly affected the Leeuwin Current earlier in its history, the resolution afforded by younger stratigraphic sections as well as geochemical data preserved in modern and fossil coral skeletons has allowed researchers to investigate the climate-current relationship at two increasingly finer temporal scales as the recent is approached.

The first of these is Milankovitch-style orbital forcing of climate, which has been shown to affect Leeuwin Current activity on scales of 10–100 Ka at least since the onset of Pleistocene time, two million years ago. These cycles were likely responsible for the pronounced variability in the strength of the Leeuwin Current during the Pleistocene as well as the changeover to a carbonate-dominated, subtropical-tropical sedimentary regime in coastal Western Australia during the Middle Pleistocene. The best-studied of the orbital-scale events are the Last Interglacial and Last Glacial Maximum. Sedimentary deposits and fossil assemblages from each interval have yielded information about SST variability and estimates of the strength of the Leeuwin Current. Range expansions and contractions of important marine benthic taxa in response to current variability have been documented from coastal and offshore deposits produced during each interval.

The finest temporal resolution of Leeuwin Current history comes from climate proxies obtained by geochemical analyses of fossil and modern coral skeletons. Perhaps it is this history that is most relevant to issues of contemporary marine management. The coral proxy record shows clearly that the Leeuwin Current is sensitive to changes in global climate (*e.g.*, El Niño-La Niña events) as well as subtle changes in regional climate (*e.g.*, impact of volcanic eruptions), both of which operate over human timescales. Given the sensitivity apparent from the recent geological past, the Leeuwin Current is certain to respond to anthropogenically induced warming over this century. Hence continued application of geological analogues (using the recent geological past to inform predictions of the biologic response to future change) and climate modelling (to predict the timing and magnitude of that change) remain an essential, albeit challenging research arena.

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Northern Sources of the Leeuwin Current and the "Holloway Current" on the North West Shelf

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Abstract

This paper reviews the northern sources of the Leeuwin Current and related circulation on the North West Shelf, north of where it consolidates into its well-known poleward boundary current structure off North West Cape, Australia.

This review finds that relatively warm, low salinity waters enter the Indonesian-Australian Basin through two major remote northern sources. One is tropical Pacific Ocean water emanating from the South East Asian seas via the Lombok, Ombai and Timor Straits. The other is tropical northwest Indian Ocean water via the South Java Current within the 5–10° S zone off the Sumatra and Java coasts.

At the broadest scales, both sources undergo circuitous routes and associated evaporation and cooling before entering the head of the Leeuwin Current off North West Cape.

It is largely unresolved as to how close to the North West Shelf coast the Leeuwin Current's source waters flow. However, earlier oceanographic studies, supported by more recently collected data presented in this paper, indicate that at least during the low wind conditions of the Southern Hemisphere autumn, a reasonably well-defined, southwestward coastal flow occurs along the shelf and shelf break. An explanation previously suggested is that this current is driven by the steric height gradient produced by local surface heating, and we propose here to name it the Holloway Current in honour of the late Dr Peter Holloway.

Keywords: Leeuwin Current, North West Shelf, Indonesian Throughflow, Holloway Current.

Introduction

To provide the broad-scale context of this review, we begin by presenting a picture (Figure 1, adapted from Domingues *et al.* 2007) of the relevant major current systems known to operate in the southeast Indian Ocean. The key features to note in the northern portion are the Indonesian Throughflow via the Lombok, Ombai and Timor Straits, the semi-annually reversing South Java Current, the South Equatorial Current and the Eastern Gyral Current, which bifurcates north and south en route to northwest Australia. South of North West Cape, the prominent flows are the Leeuwin Current, Leeuwin Undercurrent, West Australian Current and South Indian Current.

Kronberg (2004) and Domingues (2006) describe the seasonal wind patterns over the region between northwest Australia and the Indonesian archipelago in the context of their importance to the hydrodynamics of the North West Shelf and adjacent Indonesian-Australian Basin region. The wind patterns are dominated by the changing monsoons: the Summer Monsoon (generally December-April) and Winter Monsoon (generally June–October) (Figure 2). West-southwesterly winds dominate during the austral summer (December–February). Winds then weaken to almost zero in March, to be followed by a weak to moderate April period and relatively strong east-southeasterlies associated with the well known Southeast Trade Wind pattern until about September. The winds then relax and turn again to the Summer Monsoon pattern. These wind patterns play a very important role in the dynamics of the underlying ocean by inducing Ekman flows which interact with the regional current systems. The interplay between Ekman induced and geostropically driven currents is an important feature.

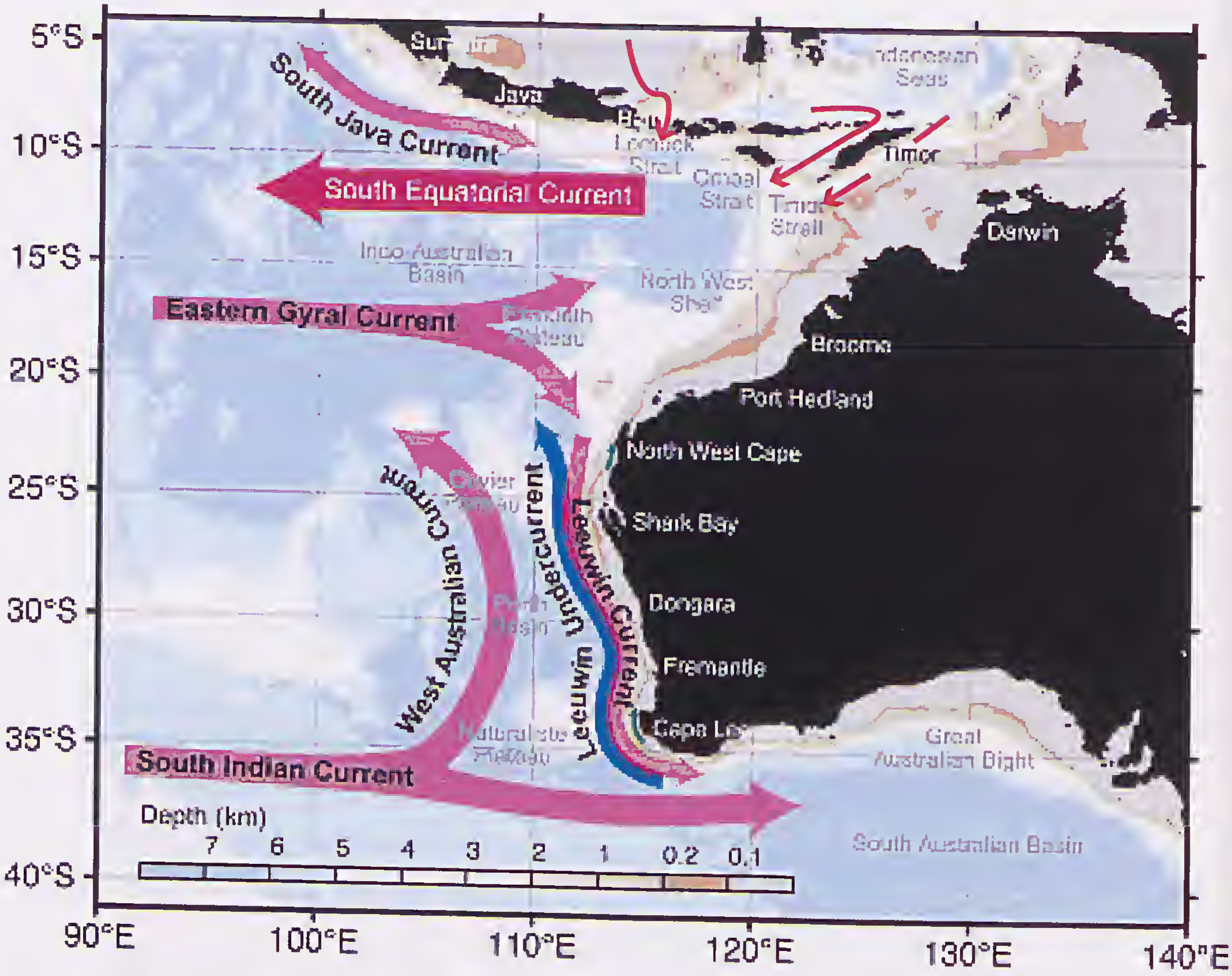


Figure 1. Major current systems in the southeast Indian Ocean, including the Indonesian Throughflow emanating from the Lombok, Ombai and Timor Straits. (adapted from Domingues *et al.* 2007).

This paper's focus is to review the northern sources of the Leeuwin Current and the circulation patterns of the North West Shelf that influence these sources en route to feeding the head of the Leeuwin Current off North West Cape. The sub-tropical sources (Domingues 2006) and Leeuwin Undercurrent (Thompson 1984, 1987; Smith *et al.* 1991; Pattiaratchi 2006; Domingues 2006) are not addressed in this paper.

Over 100 years ago, marine biologists postulated the existence of an eastern boundary current of tropical and sub-tropical water propagating southwards along the Western Australian coastline (Pearce & Cresswell 1985). Subsequently it has been found that this current turns eastward when it reaches the Southern Ocean and continues to flow along the southern Australian coastline until it reaches Tasmania, where it turns southwards to form the Zeehan Current (Ridgeway & Condie 2004). Domingues (2006) investigated where the Leeuwin Current derives its major sources of water, concluding that these are in the Indonesian Throughflow (tropical waters of Pacific Ocean origin), South Java Current (tropical waters of Indian Ocean origin) and sub-tropical waters in sub-surface intensified eastward jets of the sub-tropical Indian Ocean gyre. Kronberg (2004) examined aspects of seasonal circulation over the North West Shelf and its possible impact on the larger scale ocean circulation. Of particular interest was the origin of the seasonal maximum in the Leeuwin Current, which is observed around May. Pattiaratchi & Buchan (1991) and Feng *et al.* (2003) note that the broad scale drivers of the Leeuwin Current are subjected to ocean scale ENSO variability at inter-annual scales, with the current strengthening during La Nina years and weakening during El Nino years.

Leeuwin Current historical context

The Leeuwin Current is driven by a strong meridional pressure gradient, which is fundamentally established by the steric height difference between the relatively buoyant surface waters off northwest Australia and relatively denser (cooler and higher in salinity) surface waters off southwest Australia. This height difference is estimated to be as large as 0.5 m at its seasonal maximum (Pattiaratchi 2006). The Leeuwin Current flows poleward

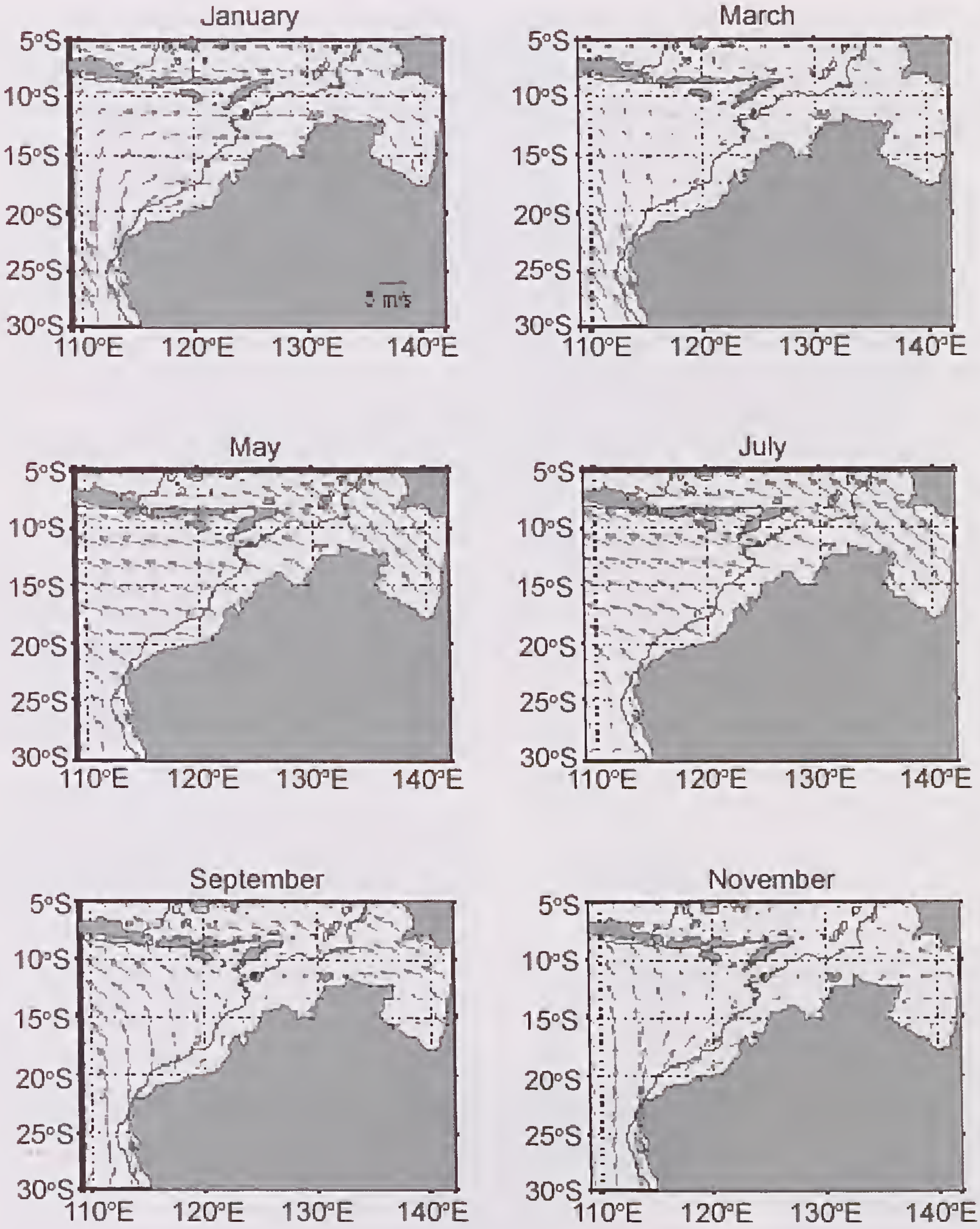


Figure 2. Major wind patterns over the North West Shelf and Indonesian-Australian Basin region (from Kronberg 2004).

despite, and in opposition to, prevailing equatorward winds off the coast. Godfrey & Ridgway (1985) examined the alongshore momentum balance between northwest and southwest Australia, indicating that the pressure gradient dominates in the austral autumn-spring, being at its strongest during May–June, and that northward winds dominate during spring-summer. Seasonal wind stress manages to modulate the Leeuwin Current, allowing it to be at its maximum strength in winter when opposing winds are at their weakest. In spring–summer, coastal winds drive opposing coastal counter currents of relatively high salinity and low temperature, confirmed at several locations, variously impeding or forcing the Leeuwin Current offshore (Rochford 1969; Cresswell & Golding 1980; Cresswell *et al.* 1985, 1989; Smith *et al.* 1991; Gersbach *et al.* 1999; Taylor & Pearce 1999; Pearce

& Pattiaratchi 1999; van Hazel 2001; Woo *et al.* 2006a,b; Pattiaratchi 2007; Akhir 2008; Woo & Pattiaratchi submitted). These counter currents are associated with sporadic upwelling and resulting coastally enhanced nutrient levels, phytoplankton biomass and primary production, as exemplified by Hanson *et al.* (2005) for the Ningaloo Current (Taylor & Pearce 1999) off North West Cape and reviewed generally for Western Australia by Pattiaratchi (2006). Notwithstanding this, the Leeuwin Current generally suppresses broad-scale coastal upwelling of the intensity that features off the other two equivalent continental west coastlines of the southern hemisphere (South America and South Africa) where colder, higher salinity equatorward coastal flows dominate throughout the year (Pearce 1991). As a result, although the prevailing wind regime is similar to the highly productive coastal waters of these other eastern ocean margins, the Western Australian coastal waters have relatively low nutrient levels and associated primary production, being oligotrophic by comparison (Pattiaratchi 2007).

The Leeuwin Current's capacity to carry tropically derived waters and associated biological propagules (Simpson 1991; Hatcher 1991) is responsible for the presence of a globally recognised and unique marine biodiversity hotspot (Roberts *et al.* 2002) off the central west coast of Western Australia, characterised by a mix of tropical and temperate species. It is also responsible for the presence of tropical species off the south coast of Western Australia. The Leeuwin Current is therefore a fundamentally important mechanism underpinning the marine biodiversity of the region. It also plays a strong role in local climate through its influence on sea surface temperatures and coupled atmospheric properties off the coast (Weaver 1990; Gentilli 1991; Pattiaratchi & Buchan 1991; Telcik 2004).

The Leeuwin Current begins its distinct flow as a coherent boundary current in the vicinity of North West Cape, at about 22° S. At this Leeuwin Current head region, it has typical properties of approximately 150 m deep, 0.5 m s^{-1}, 34.9 psu, 24 °C and 1023.6 kg m^{-3}, and is slightly more saline and cooler than the waters of the Indonesian Throughflow and South Java Current to the north (Domingues 2006). By the time it passes 34° S, the Leeuwin Current's properties undergo a transition to approximately 300 m depth, 1.5 m s^{-1}, 35.55 psu, 18 °C and 1025.7 kg m^{-3}, having been augmented by geostrophic inflows of sub-tropical Indian Ocean water (Domingues 2006; Godfrey & Weaver 1991). It is generally <100 km wide along its length and strongly meandering (Thomson 1984; Smith *et al.* 1991; Pearce & Griffiths 1991), regularly breaking out to sea in eddies and other associated dynamical instabilities (Waite *et al.* 2007). The Leeuwin Current signature extends from North West Shelf to Tasmania, forming the longest boundary current in the world (Ridgway & Condie 2004). Further details on the anatomy and dynamics of the Leeuwin Current can be found in Waite *et al.* (2007).

Northern sources of the Leeuwin Current

The major northern sources of the Leeuwin Current were reviewed and analysed by Domingues (2006) and Domingues *et al.* (2007). They used the 1994-96 WOCE ICM6 experiment observations at 22° S and numerically modelled tracking of particles (released in the upper 600 m of the Pacific and Indian oceans) from the 1/6 deg. Los Alamos National Laboratory Parallel Ocean Program model (POP11B) for the simulation period 1993–1997 (Figure 3).

This work was conducted in conjunction with reviews of past studies on associated volume transports of the Leeuwin Current's source waters and regional circulation patterns. It supports and supplements earlier studies (*e.g.*, Godfrey 1996; Bray *et al.* 1997; Potemra *et al.* 2002; Wijffels *et al.* 2002; Feng & Wijffels 2002; Wijffels &

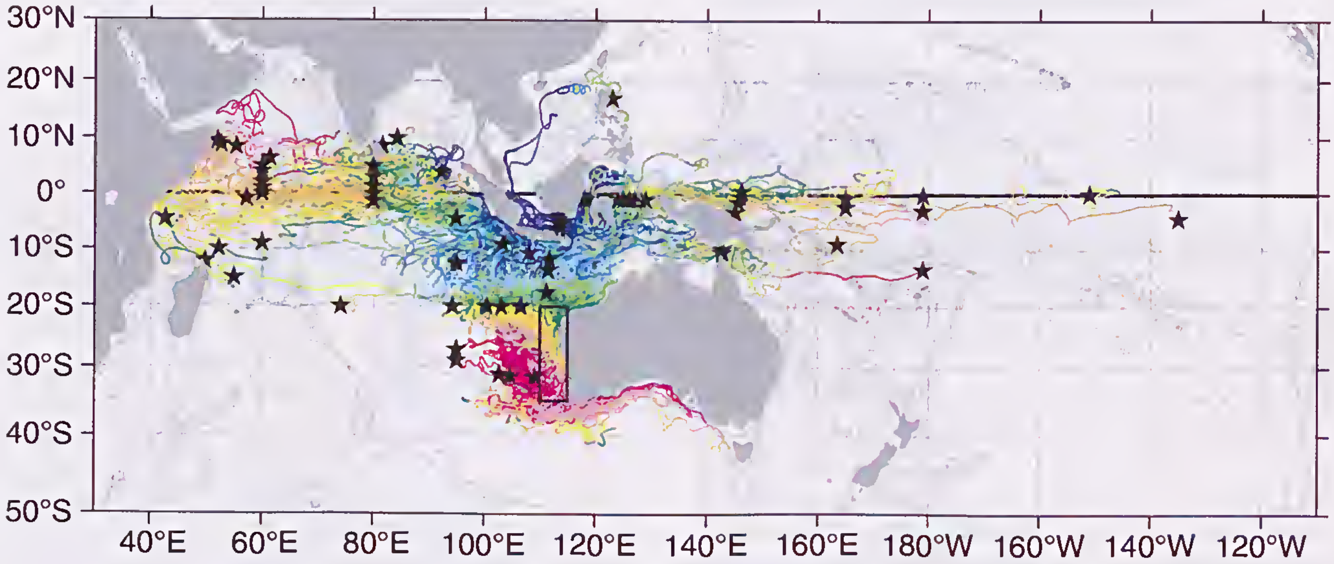


Figure 3. Northern tropical sources of the Leeuwin Current, as indicated by particle trajectories analysed by Domingues *et al.* (2007) from model output of the Los Alamos National Laboratory Parallel Ocean Programme run POP11B (1993-97). The stars represent particle trajectory release points (all with start depths < 600m). The coloured lines show the paths traversed by the particles. Different colours along the lines represent different salinities. The particles shown were those that found their way into the black box drawn off Western Australia, representing the Leeuwin Current.

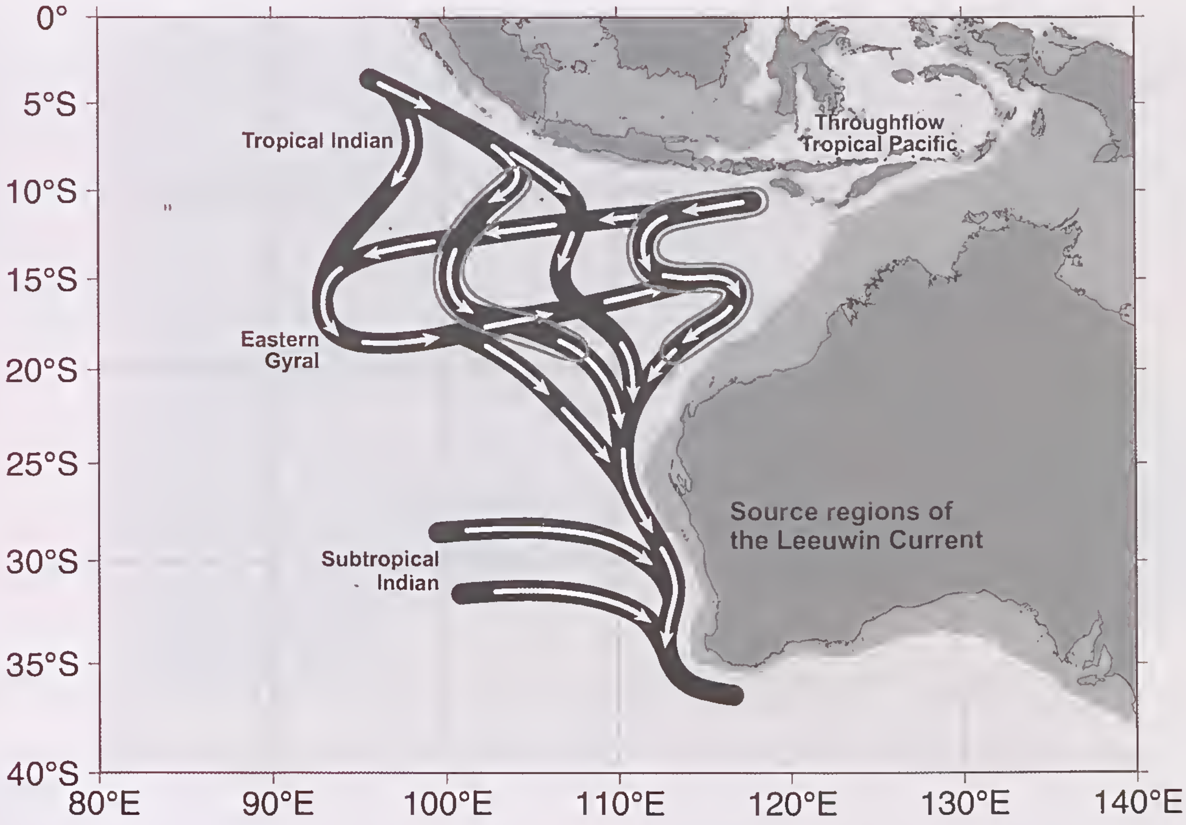
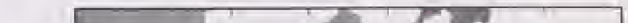


Figure 4. Schematic diagram (from Domingues *et al.* 2007) of the upper circulation of the southeast Indian Ocean near Australia associated with the source regions of the Leeuwin Current, as per the results of the Domingues *et al.* (2007) POP trajectory analyses in Figure 3.

Meyers 2004) in showing that the equatorial Pacific Ocean region provides a major northern source of water for the Leeuwin Current, carrying tropical Pacific Ocean water into the Indonesian-Australian Basin via the Lombok, Ombai and Timor Straits.

Domingues (2006) and Domingues *et al.* (2007) also used the POP model particle tracks to identify the other major northern source for the Leeuwin Current as the Indian Ocean, where tropical water is derived from between northeast Africa and Indonesia. Particles find their way to the head of the Leeuwin Current off North West Cape mainly via the South Java Current (Quadfasel & Cresswell 1992; Meyers *et al.* 1995), which is a boundary current that semi-annually reverses to flow prominently southeastward off Sumatra and Java around May to November. At these times, the South Java Current is principally a response to coastal and equatorial Kelvin waves, or Wyrtki Jets, (driving the Equatorial Counter Current) forced by westerly wind bursts during the monsoon transitions in the equatorial Indian Ocean (Wijffels *et al.* 1996; Sprintall *et al.* 1999). The other, lesser, source for the South Java Current is the Indian Monsoon Current that is locally generated by winds of the Indian Monsoon (Wijffels *et al.* 1996).

At the broadest scales, Domingues (2006) and Domingues *et al.* (2007) also investigated the pathways that these respective sources most likely follow en route to the head of the Leeuwin Current, concluding that both undergo circuitous routes and associated evaporation



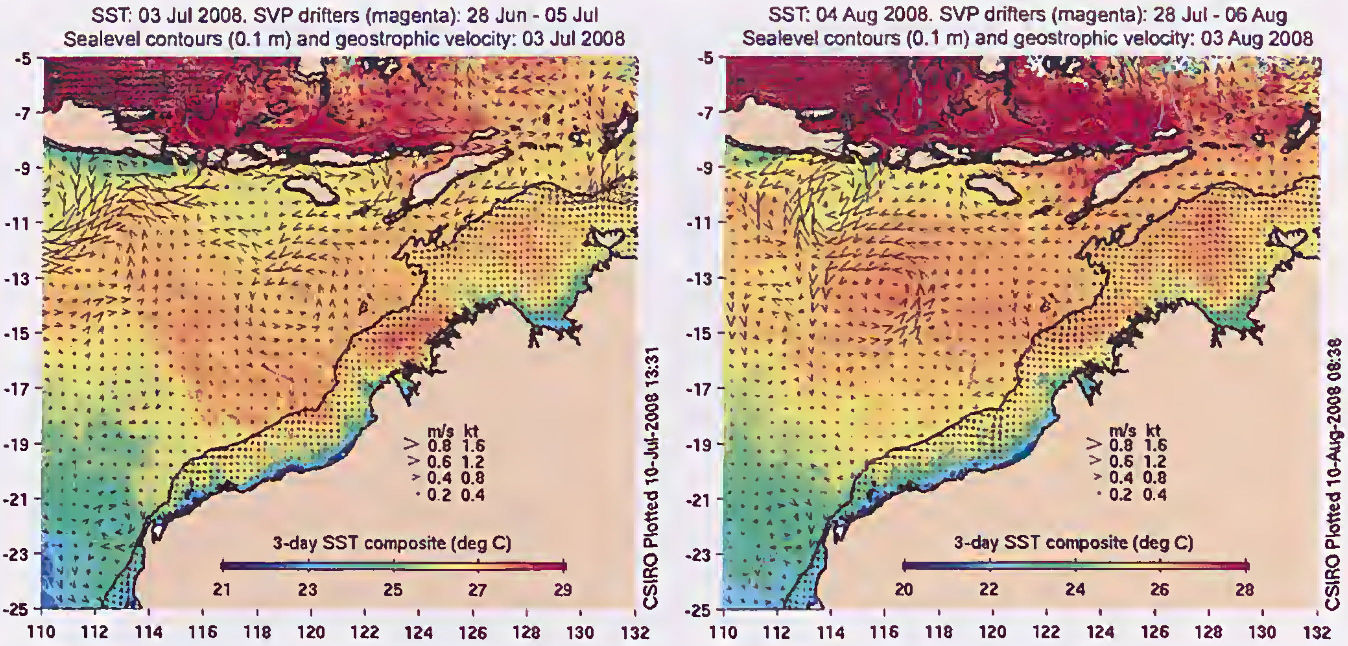

SST: 03 Jul 2008. SVP drifters (magenta): 28 Jun - 05 Jul
Sealevel contours (0.1 m) and geostrophic velocity: 03 Jul 2008
m/s kt
0.8 1.6
0.6 1.2
0.4 0.8
0.2 0.4
3-day SST composite (deg C)
21 23 25 27 29
CSIRO Plotted 10-Jul-2008 13:31
SST: 04 Aug 2008. SVP drifters (magenta): 28 Jul - 06 Aug
Sealevel contours (0.1 m) and geostrophic velocity: 03 Aug 2008
3-day SST composite (deg C)
20 22 24 26 28
CSIRO Plotted 10-Aug-2008 08:38
-5 -7 -9 -11 -13 -15 -17 -19 -21 -23 -25
110 112 114 116 118 120 122 124 126 128 130 132

Figure 6. Satellite images for 3 July showing a very prominent eddy centred at about 120° E , 14° S which has moved westwards a distance of about 300km by 3 August 2008. This is equivalent to a westward propagation speed of 10 km day^{-1} or 0.1 m s^{-1}.

and cooling before passing North West Cape (Figure 4). In the upper 100 m of the water column, some of the water that emerges from the Indonesian Throughflow joins the westward flowing South Equatorial Current (south of the Indonesian Archipelago), within the 10–15° S zone. The flow geostrophically traverses that current and becomes part of the southern branch of the Eastern Gyral Current, which flows eastward within the 15–20° S zone. As the Eastern Gyral Current approaches the northwest coast of Australia, it bifurcates north and south, with the southern branch feeding the head of the Leeuwin Current.

Two other characteristic pathways for the source waters are ones that emanate from the Indonesian Throughflow and the other from the South Java Current, with Domingues *et al.* (2007) referring to them as the direct offshore "C" route and indirect onshore "S" route respectively. All pathways meet on the North West Shelf and become a surface poleward boundary flow which is strongest from April to July. The idea that the Leeuwin current is supplied with waters directly from the Timor Strait is not supported by the modelled particle tracks, but this may be as a result of a model bias that overestimates the flow rate passing through Ombai Strait (Domingues 2006)

The mean geostrophic velocity and transport associated with the Indonesian Throughflow were examined by Wijffels *et al.* (2008) on the basis of 20 years of eXpendable BathyThermograph (XBT) data. Their schematic (Figure 5) provides a recent assessment of the various volume fluxes associated with the main currents in the region

Circulation on the North West Shelf

There appear to be very few observational, numerical or analytical studies addressing the detailed dynamical characteristics associated with the overall progression of Indonesian Throughflow and South Java Current waters through to the head of the Leeuwin Cuurent (Domingues *et al.* 2007). As such, this aspect of the dynamics of the region is yet to be accurately resolved. Some studies have analysed satellite altimeter data to discern eddy features in the region. For example, Feng & Wijffels (2002) suggest the occurrence of important baroclinic instability features in the South Equatorial Current zone, which draw their energy from the available potential energy associated with the Throughflow. The eddies are typically 150–200 km in diameter with current speeds in the range 0.4–0.8 m s^{-1}. They propagate westwards at speeds of up to 0.2 m s^{-1} and remain coherent over 40–80 day periods. An inspection of satellite images for the region of interest shows that these eddies are nearly always present. A typical example is shown in Figure 6. Bray *et al.* (1997) examined WOCE and JADE hydrographic observations, in conjunction with TOPEX/POSEIDON altimeter data, finding westward propagating features between 8° S and 13° S, generally consistent with those reported by Feng & Wijffels (2002). The eddies were simulated by Nof *et al.* 2002, using analytical models which support the idea that they are caused by a baroclinic instability mechanism.

Further south in the latitude band 20°–30° S, Fang & Morrow (2003) described the characteristics of eddies originating in the Leeuwin Current, again using TOPEX/POSEIDON altimeter data. In the period 1995 to 2000 they tracked 37 warm, long-lived eddies, some travelling west a distance of 2500km at speeds ranging from 0.02 to 0.15 m s^{-1}. In the process, they transfer low-density Indonesian Throughflow and Leeuwin Current source waters, into the southeast Indian Ocean. Most of these eddies are spawned during the period May – June, when the Leeuwin Current is most intense, suggesting an instability mechanism perhaps triggered by topographic features.

Although previous observations over the North West Shelf have been relatively limited and spatially

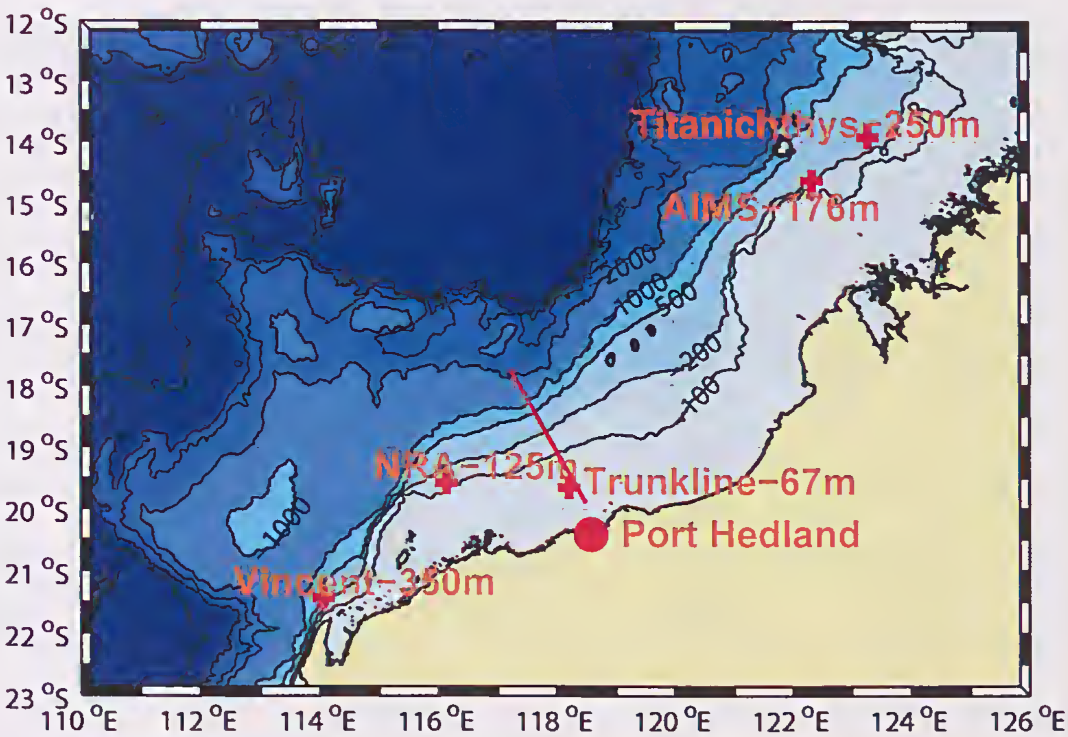
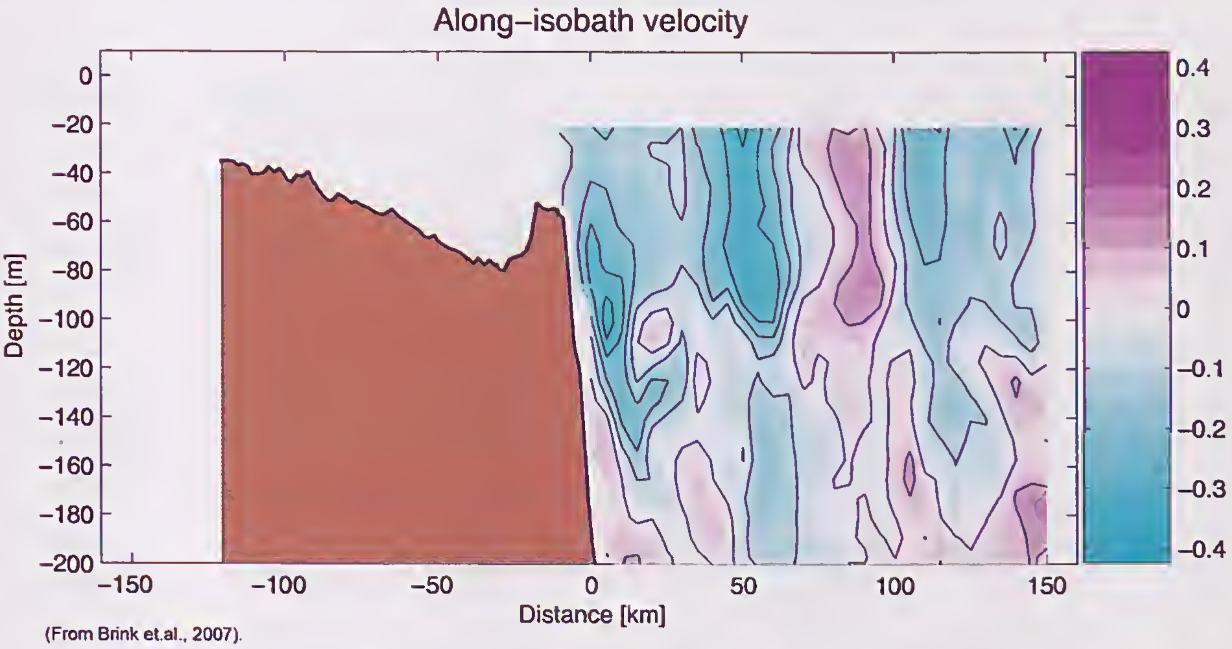


Figure 7. Current meter locations over and adjacent to the North West Shelf of Australia (courtesy of RPS MetOcean on behalf of Inpex Browse Ltd, Woodside Energy Ltd (Perth) and the Australian Institute of Marine Sciences (AIMS)). Also shown is the CTD and ADCP transect (red line) of Brink *et al.* (2007).



(From Brink et.al., 2007).

Figure 8. Alongshore current at the transect shown in Figure 7 representative of the flow in June- July, 2003.

constrained, the measurements analysed by Holloway & Nye (1985) nonetheless suggest a propensity for flow over this shelf to be a potentially important contribution to the Leeuwin Current. Holloway & Nye (1985) analysed 19 months of current meter data (1982/83) collected over the North West Shelf in water depths between 40 and 260 m in the region 114.5–116.5° E and 19.5–21.2° S. Reasonably strong southwestward flow was evident, being strongest during February-July of both years and stronger than could be accounted for by wind stress alone. Holloway & Nye (1985) reasoned this to be the Leeuwin Current on the North West Shelf driven by steric height gradient in opposition to wind stress, consistent with the ideas of Godfrey & Ridway (1985). Holloway & Nye (1985) also noted the occurrence of weak upwelling events in both summer and winter

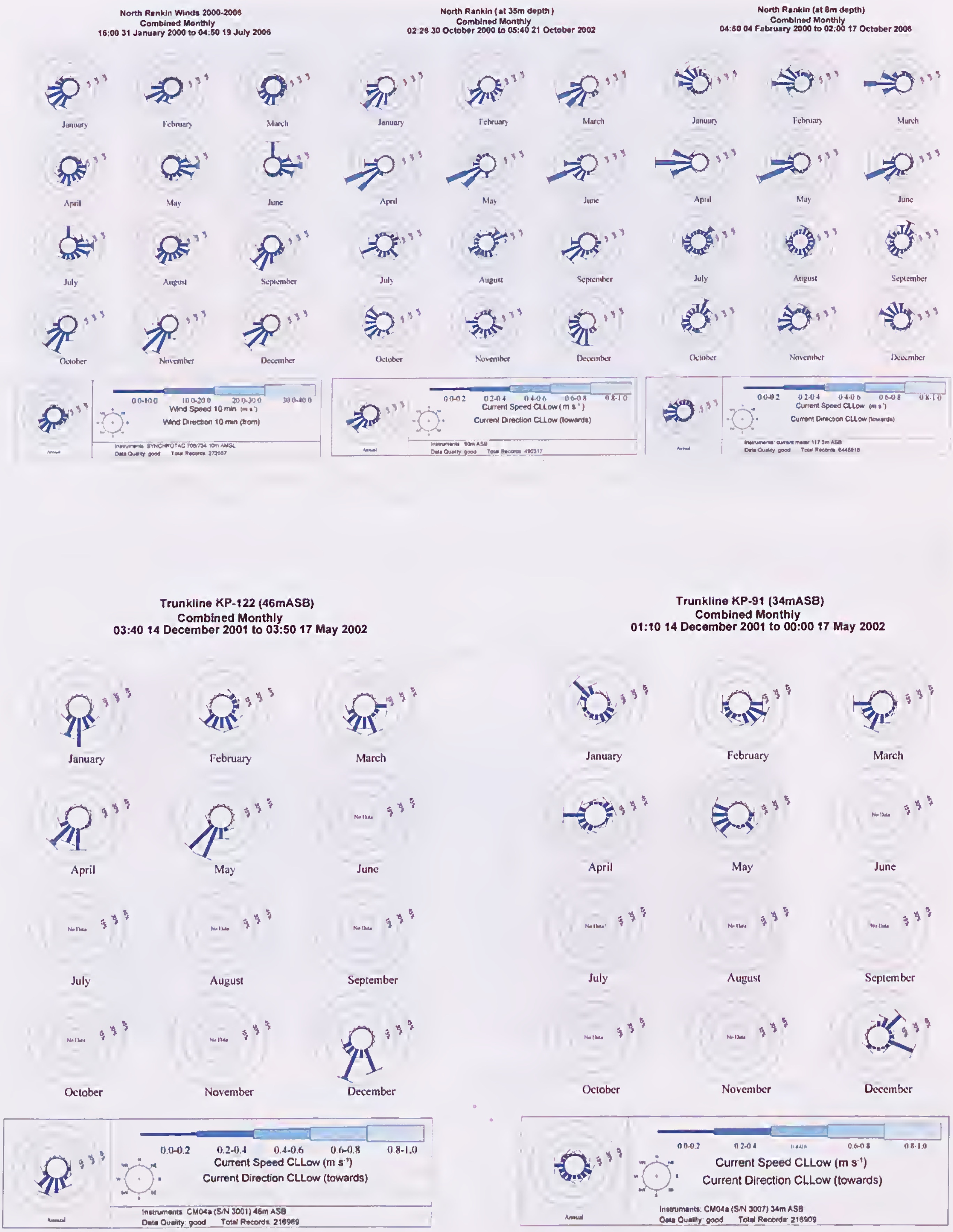
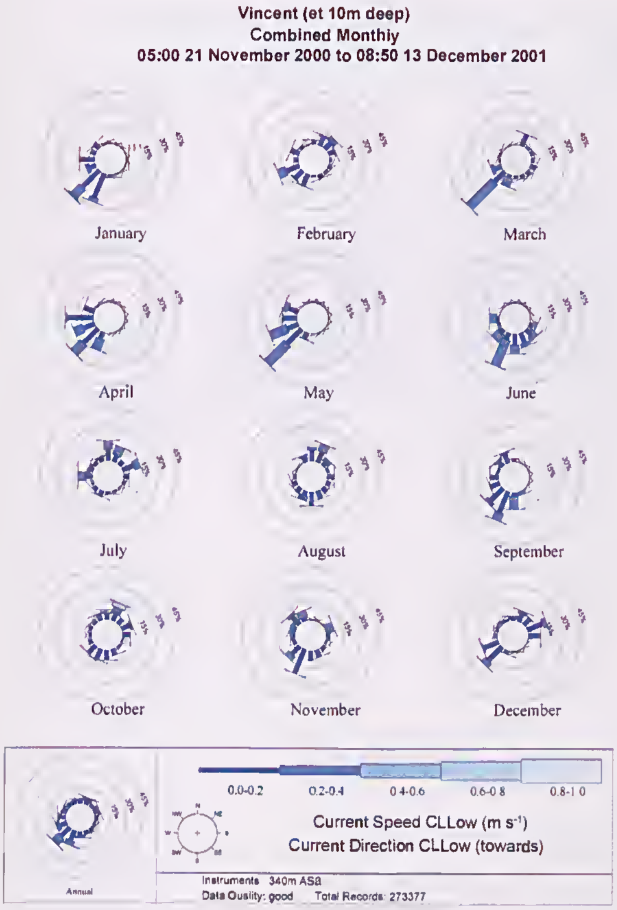
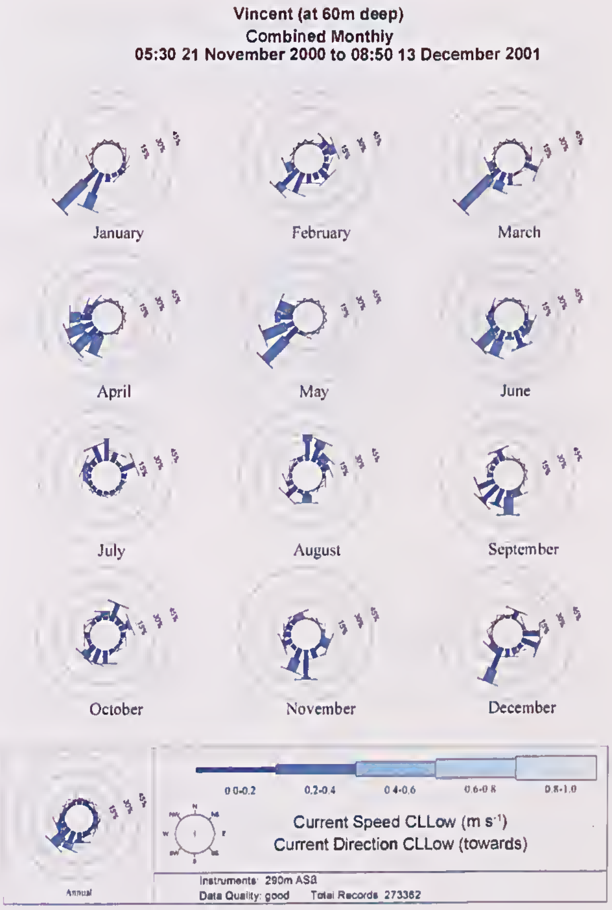
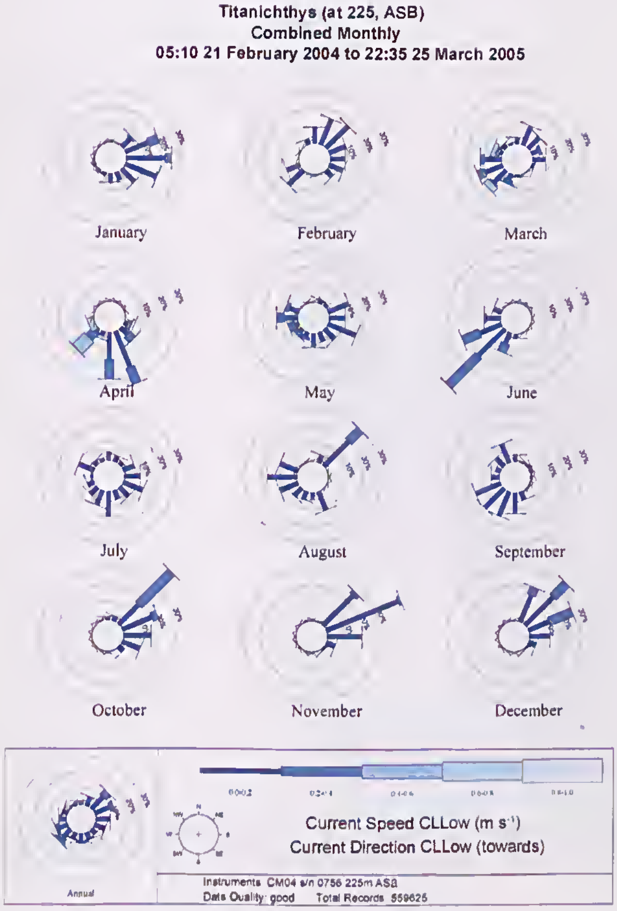
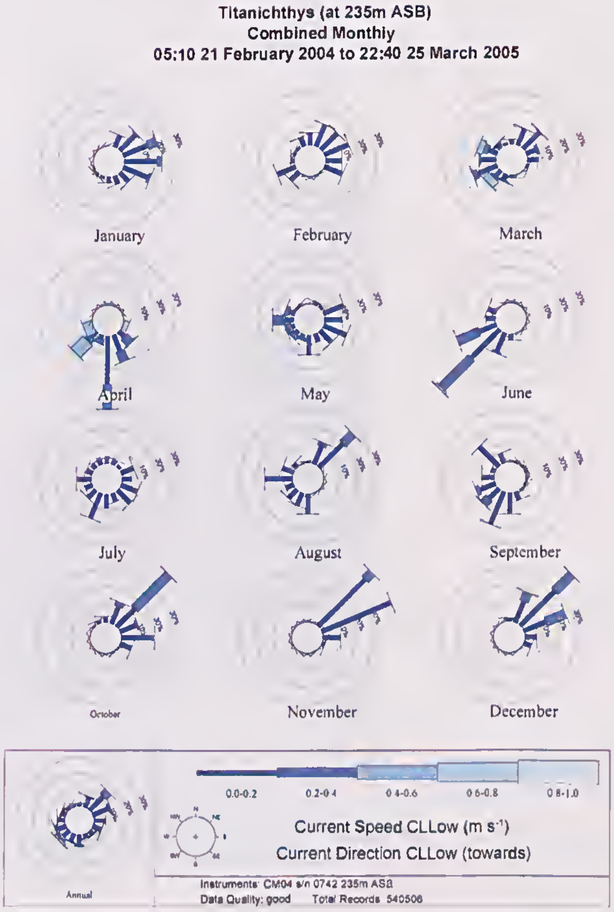


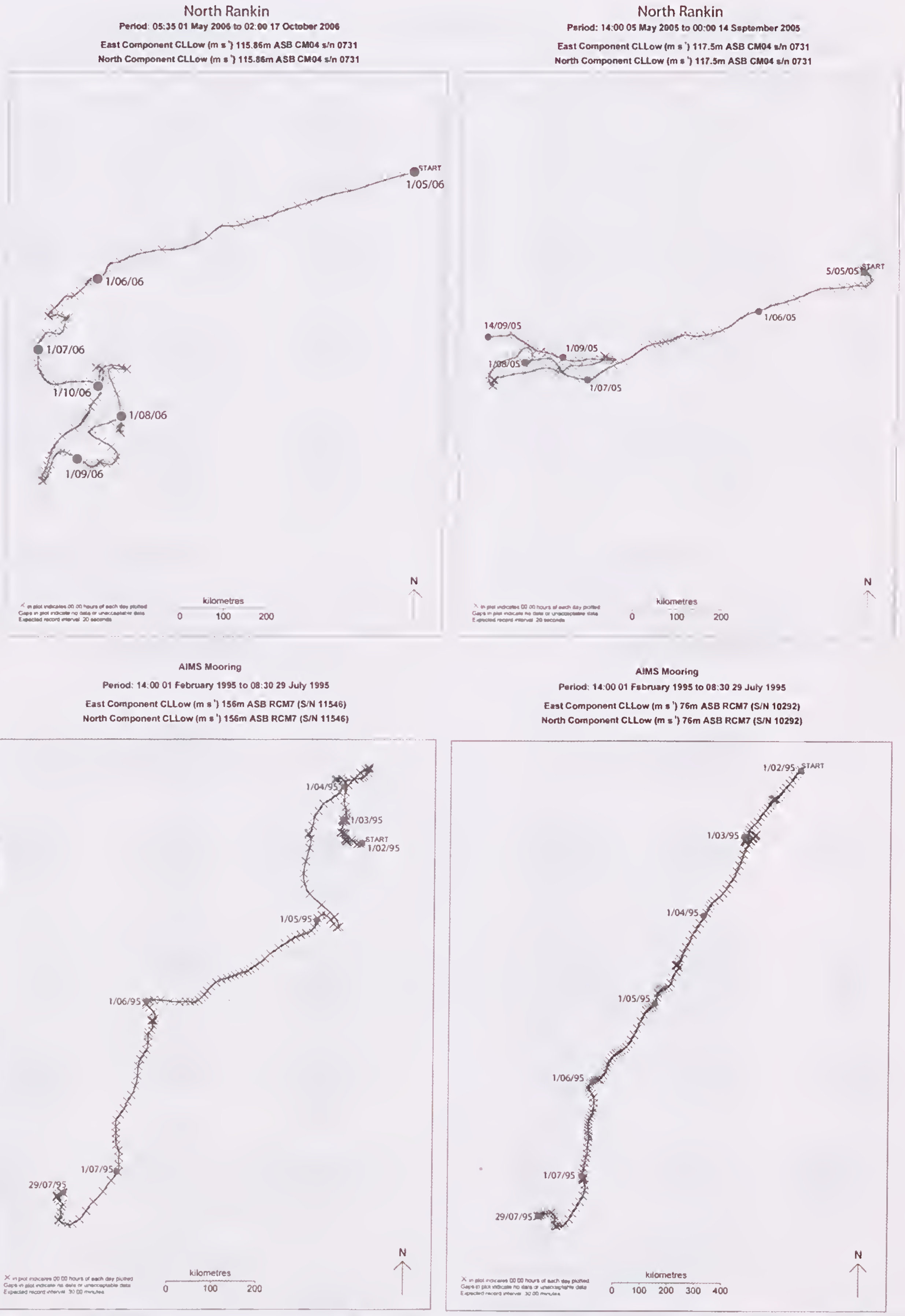
Figure 9. Combined monthly averaged current meter for data collected at the sites shown in Figure 7. For North Rankin, monthly averaged wind roses (directions from which wind is blowing) are also presented, showing winds predominantly from the southwest during September–February, and then weakening in March to April/May.


Vincent (at 10m deep)
Combined Monthly
05:00 21 November 2000 to 08:50 13 December 2001
January
February
March
April
May
June
July
August
September
October
November
December
Annual
0.0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1.0
N
NE
E
SE
S
SW
W
NW
Current Speed CLLow (m s⁻¹)
Current Direction CLLow (towards)
Instruments 340m ASB
Data Quality: good
Total Records: 273377


Vincent (at 60m deep)
Combined Monthly
05:30 21 November 2000 to 08:50 13 December 2001
January
February
March
April
May
June
July
August
September
October
November
December
Annual
0.0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1.0
N
NE
E
SE
S
SW
W
NW
Current Speed CLLow (m s⁻¹)
Current Direction CLLow (towards)
Instruments: 290m ASB
Data Quality: good
Total Records 273362


Titanichthys (at 225, ASB)
Combined Monthly
05:10 21 February 2004 to 22:35 25 March 2005
January
February
March
April
May
June
July
August
September
October
November
December
Annual
0.0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1.0
N
NE
E
SE
S
SW
W
NW
Current Speed CLLow (m s⁻¹)
Current Direction CLLow (towards)
Instruments CM04 s/n 0756 225m ASB
Data Quality: good
Total Records 559625


Titanichthys (at 235m ASB)
Combined Monthly
05:10 21 February 2004 to 22:40 25 March 2005
January
February
March
April
May
June
July
August
September
October
November
December
Annual
0.0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1.0
N
NE
E
SE
S
SW
W
NW
Current Speed CLLow (m s⁻¹)
Current Direction CLLow (towards)
Instruments: CM04 s/n 0742 235m ASB
Data Quality: good
Total Records 540506



North Rankin
Period: 05:35 01 May 2006 to 02:00 17 October 2006
East Component CLLow (m s⁻¹) 115.86m ASB CM04 s/n 0731
North Component CLLow (m s⁻¹) 115.86m ASB CM04 s/n 0731

North Rankin
Period: 14:00 05 May 2005 to 00:00 14 September 2005
East Component CLLow (m s⁻¹) 117.5m ASB CM04 s/n 0731
North Component CLLow (m s⁻¹) 117.5m ASB CM04 s/n 0731

AIMS Mooring
Period: 14:00 01 February 1995 to 08:30 29 July 1995
East Component CLLow (m s⁻¹) 156m ASB RCM7 (S/N 11546)
North Component CLLow (m s⁻¹) 156m ASB RCM7 (S/N 11546)

AIMS Mooring
Period: 14:00 01 February 1995 to 08:30 29 July 1995
East Component CLLow (m s⁻¹) 76m ASB RCM7 (S/N 10292)
North Component CLLow (m s⁻¹) 76m ASB RCM7 (S/N 10292)

START
1/05/06
1/06/06
1/07/06
1/10/06
1/08/06
1/09/06
× in plot indicates 00:00 hours of each day plotted
Gaps in plot indicate no data or unacceptable data
Expected record interval 20 seconds
kilometres
0
100
200
N
5/05/05
START
1/06/05
14/09/05
1/09/05
1/08/05
1/07/05
× in plot indicates 00:00 hours of each day plotted
Gaps in plot indicate no data or unacceptable data
Expected record interval 20 seconds
kilometres
0
100
200
N
1/04/95
1/03/95
START
1/02/95
1/05/95
1/06/95
1/07/95
29/07/95
× in plot indicates 00:00 hours of each day plotted
Gaps in plot indicate no data or unacceptable data
Expected record interval 30.00 minutes
kilometres
0
100
200
N
1/02/95
START
1/03/95
1/04/95
1/05/95
1/06/95
1/07/95
29/07/95
× in plot indicates 00:00 hours of each day plotted
Gaps in plot indicate no data or unacceptable data
Expected record interval 30.00 minutes
kilometres
0
100
200
300
400
N

Figure 10. Continuous vector plots at (a) North Rankin at about 10 m depth showing a persistent south-westerly flow in May, and variable flow later, and (b) further north at the AIMS site, the flow at 100 m and 20 m depth is persistently south westwards for the period March to June.

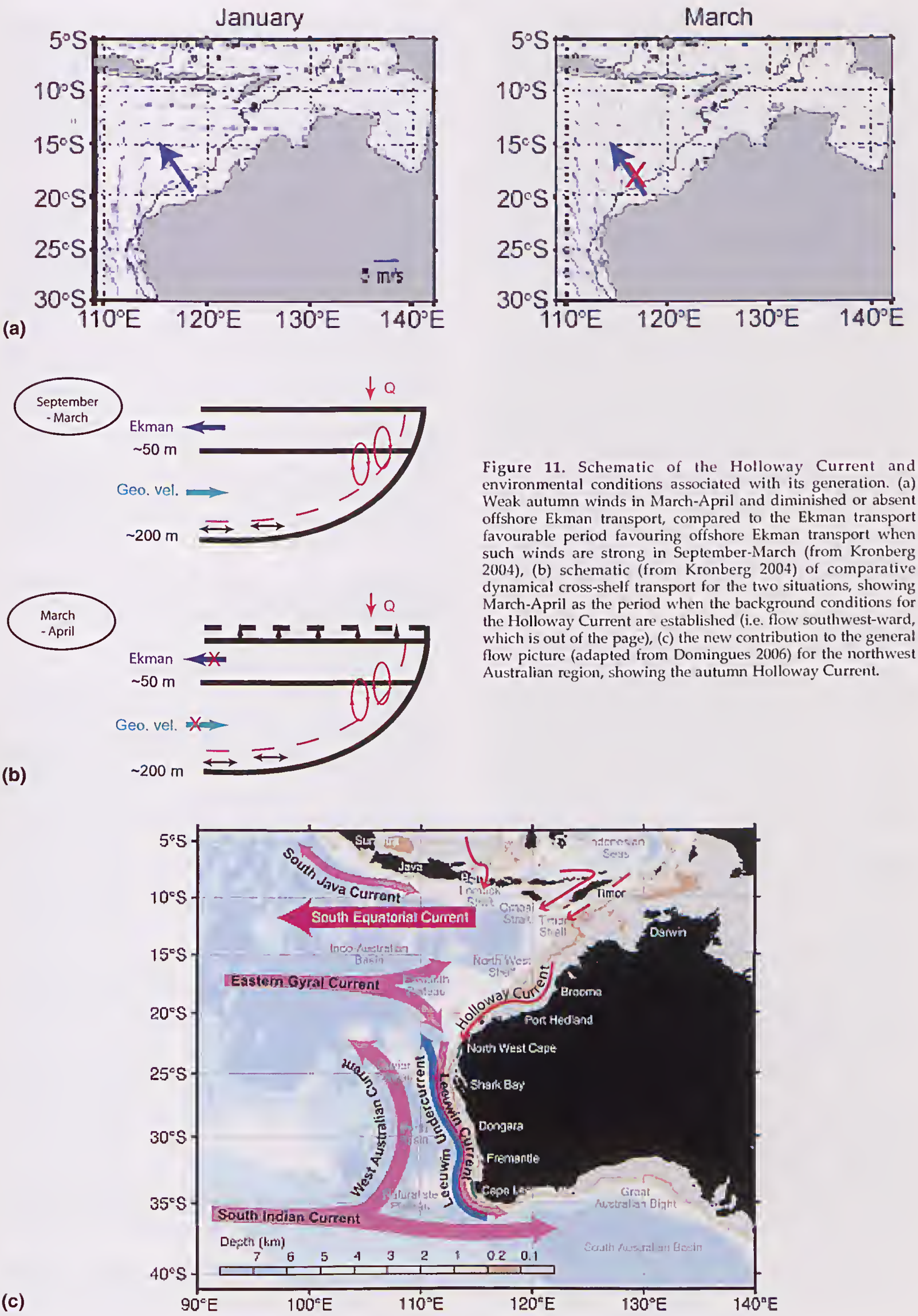


Figure 11. Schematic of the Holloway Current and environmental conditions associated with its generation. (a) Weak autumn winds in March-April and diminished or absent offshore Ekman transport, compared to the Ekman transport favourable period favouring offshore Ekman transport when such winds are strong in September-March (from Kronberg 2004), (b) schematic (from Kronberg 2004) of comparative dynamical cross-shelf transport for the two situations, showing March-April as the period when the background conditions for the Holloway Current are established (i.e. flow southwest-ward, which is out of the page), (c) the new contribution to the general flow picture (adapted from Domingues 2006) for the northwest Australian region, showing the autumn Holloway Current.

months, suggesting the cause to be southwesterly winds of sufficient strength to overcome the background steric height gradient.

In a subsequent study based on NW/SE oriented cross-shelf and slope transects of ADCP and CTD measurements centred at about 17° S and 19° S, Holloway (1995) found a distinct southwestward-flowing current in the months May and June. The current was broad (250 km at 17° S), at least 440 m deep and relatively weak (0.2 m s $^{-1}$), but the transport of about 4 x 10 ^{6} m^{3} s $^{-1}$ is similar to the range of values for the main Leeuwin Current (Smith *et al* 1991). In the same study and based on moored current meter data in the Timor Sea (~ 12° S), Holloway (1995) reported a weak poleward flow for much of the year, but strongest from January to April.

Holloway & Nye's (1985) and Holloway's (1995) results were reinforced by the investigation of Kronberg (2004) on the seasonal circulation over the North West Shelf. This work discussed the overall variability of surface circulation and the vertical structure of integrated geostrophic flow under the action of wind, buoyancy and tide. Kronberg (2004) used *in situ* temperature data and current observations from 1999–2000 and altimeter data from TOPEX/POSEIDON to investigate the flow patterns over North West Shelf when warm water is supplied to the North West Shelf from the Arafura Sea. Kronberg (2004) concluded that during autumn, the absence of strong Ekman flow offshore allows the steric height over the shelf to build up due to local heating, causing a geostrophically-driven coastal flow towards the southwest over the North West Shelf. Kronberg referred to this feature as the Extended Leeuwin Current, consistent with the spirit of the conclusions drawn by Holloway & Nye (1985) and other studies since (Cresswell *et al.* 1993; Holloway 1995; Brink *et al.* 2007).

The recent study by Brink *et al.* (2007) examined two CTD and underway ADCP transects, at similar locations to those of Holloway (1995), at 16° S and 19° S. At the southernmost transect, shown in Figure 7, the along-isobath current (Figure 8) further confirms the existence of a southwestward current on the shelf slope. The current was weak (0.2 m s $^{-1}$) and at least 200 m deep. Further offshore a countercurrent, which was almost twice as strong, is also shown.

To supplement the previously collected data sets discussed above, we present current meter data collected at five locations (Figure 7) on or adjacent to the North West Shelf. These data were collected by RPS MetOcean and the Australian Institute of Marine Science in water depths varying from 67 to 350 m, during various periods between February 1995 and January 2007.

Monthly averaged current roses at various locations and depths shown in Figure 9 (North Rankin (water depth 125 m, instrument depths 8 and 35 m), Trunkline-KP (92 m, 34 and 46 m), Vincent (350 m, 10 and 60 m) and Titanichthys (250 m, 15 and 25 m) clearly show southwestward flow during the autumn months. At North Rankin the monthly averaged wind roses are also shown, indicating that the winds are weak in the autumn months, and blowing from the southwest against the current.

Continuous vector plots of currents at North Rankin (Figure 10) at about 10 m depth for two periods, May to September 2005 and May to October 2006, show predominantly southwestward flow during the months of May and June. In May 2006, the current speed was about 0.25 m s $^{-1}$, while in May 2005 the current speed was only 0.08 m s $^{-1}$. Further north, at the AIMS mooring (Figure 10), the flow at two depths, 20 m and 100 m, are also southwestward at speeds of about 0.12 m s $^{-1}$ and 0.08 m s $^{-1}$ respectively.

These findings are consistent with earlier results of other investigators (Holloway & Nye 1985; Holloway 1995; Brink *et. al.* 2007). We believe the mechanism driving this flow is the same as that reasoned by Kronberg (2004); *i.e.*, heating of the water column over the shelf, relatively weak winds allowing the heated water to be maintained over the shelf and not be otherwise replaced by upwellings of colder water, a consequent rise in steric height over the North West Shelf and, in turn, a geostrophic flow southwestward along the shelf. Whether this in fact represents a flow 'into' the head of the Leeuwin Current, or a seasonally occurring northward extension of where the Leeuwin Current actually starts, is open to interpretation.

We propose to formalise the name of this autumn current over the North West Shelf as the Holloway Current (Figure 11), in honour of the pioneering work by the late Dr Peter Holloway.

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Climate variability and ocean production in the Leeuwin Current system off the west coast of Western Australia

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Abstract

The strength of the Leeuwin Current (LC) and its eddy field are both strong during the austral winter and weak during the austral summer on the annual time scale, and are strong during the La Niña years and weak during the El Niño years on the interannual time scale. As the LC is a warm current, the sea surface (evaporative) heat loss off the west coast of Western Australia (WA), as well as the upper ocean stratification (mixing) and the nutrient fluxes, is also closely linked to the strength of the current. In this paper, recent studies on the temporal and spatial variability of the biophysical properties in the oligotrophic marine environment off the west coast of WA are reviewed. By analysing recent satellite chlorophyll *a* data and shipboard survey results, possible mechanisms that could be important to the variability of the ocean production off the west coast of WA are identified as: meridional erosion of the seasonal thermocline; vertical motion of the nitrocline; horizontal and vertical nutrient advection related to the LC eddy activity; *in situ* nitrification; and benthic-pelagic coupling. Potential impacts of climate change on the ocean production off the west coast of WA are hypothesized.

Keywords: ENSO; chlorophyll *a*; nitrocline; climate change; eddies

Introduction

Ocean circulation off the west coast of Western Australia (WA) is dominated by the poleward-flowing Leeuwin Current (LC). The LC is a warm ocean current that originates off the North West Cape of WA (22°S), and flows southwards along the edge of the continental shelf before turning eastwards around Cape Leeuwin (34°22'S, 115°08'E) and continuing into the Great Australian Bight (Cresswell & Golding 1980; Figure 1). The meridional pressure gradient in the southeast Indian Ocean, set up by the Indonesian Throughflow (ITF) in the tropics and by latent heat fluxes (cooling) in the mid-latitude, accounts for the existence of the LC (Thompson 1984; Godfrey & Ridgway 1985).

The LC deepens the thermocline and nitrocline off the west coast of WA (Thompson 1984), therefore suppresses productivity on the continental shelf, causing the oligotrophic marine environment off the coast. On the other hand, the LC is responsible for the existence of coral reefs as far south as 29°S (Collins *et al.* 1991) and the presence of tropical species along the west and south coasts of WA (Maxwell & Cresswell 1981; Hutchins & Pearce 1994). There are relatively large invertebrate populations off the coast, *e.g.*, western rock lobster (Panulirus Cygnus), Australia's most valuable single species fishery (Pearce & Phillips 1988; Caputi *et al.* 1995).

The LC has the strongest eddy energy among the mid-latitude eastern boundary current systems (Feng *et al.* 2005). The interannual variations of the LC and its eddy field respond to the El Nino/Southern Oscillation (ENSO) and many of the fisheries recruitments off WA are also associated with ENSO induced interannual variability (Caputi *et al.* 1995). The LC eddy field has vital influences on the marine pelagic production off the west coast of WA (*e.g.*, Hanson *et al.* 2005a; Feng *et al.* 2007; Koslow *et al.* 2008).

Understanding how the variability of the LC affects the ecosystems off the coast is crucial for the long term management of marine resources off WA. By reviewing the recent studies on the biophysical properties of the LC system and by combining satellite and *in situ* observations, this paper derives some key mechanisms that may be responsible for the nutrient dynamics in the LC system on seasonal and longer time scales, which is a first step to unveiling the full impact of the LC on the ecosystems off the WA coast.

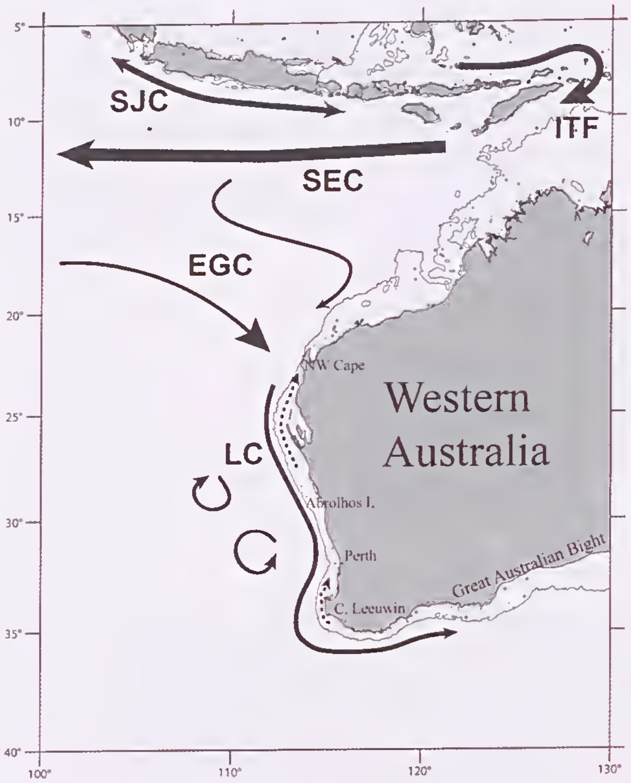


Figure 1. Regional currents in the East Indian Ocean and off the WA coast. ITF: Indonesian Throughflow; SJC: South Java Current; SEC: South Equatorial Current; EGC: East Gyral Current; LC: Leeuwin Current; NW Cape: Northwest Cape; Abrolhos I.: Abrolhos Islands; C. Leeuwin: Cape Leeuwin. The 200 m isobath of bottom bathymetry is shown as solid lines and the dashed lines denote the inshore wind-driven currents (Modified from Feng *et al.* 2003).

Physical background

The latitudinal variations of the LC are illustrated with vertical sections of average meridional velocity from a high resolution, data-assimilating numerical simulation of the ocean system (Schiller *et al.* 2008). The LC at 22°S is a broad, shallow surface current in the upper 150m, carrying waters of the tropical origin southward (Figure 2). The LC builds up its strength along the shelf break off Shark Bay and Abrolhos Islands, due to the convergence of onshore flows. The LC becomes dispersed between Abrolhos and Perth, likely due to the strong eddy activity in this region (Feng *et al.* 2005), and further south, the LC regains its strength off the Capes near 34°S. The model description of the LC is quite consistent with earlier field observations (Smith *et al.* 1991).

The LC is strong during the austral winter and weak during the austral summer (Smith *et al.* 1991; Feng *et al.* 2003), mostly due to the seasonal variations of surface winds. From a monthly upper ocean thermal climatology off the west coast of WA, the annual mean geostrophic transport of the LC is about 3.4 Sv (10^6 m^3s^{-1}) referenced to 300 m, and the LC has its peak transport during May–July (Figure 3; Feng *et al.* 2003). The seasonal variation of the LC induces a 20 cm annual variation of the Fremantle sea level. During the austral summer, pulses of northward winds overcome the meridional pressure gradient and drive the episodic northward inshore currents (Cresswell *et al.* 1989). However, coastal upwelling is only significant along narrow strips of the shelf, such as off the Capes in the south (Gersbach *et al.* 1999) and north of Abrolhos (Woo *et al.* 2006).

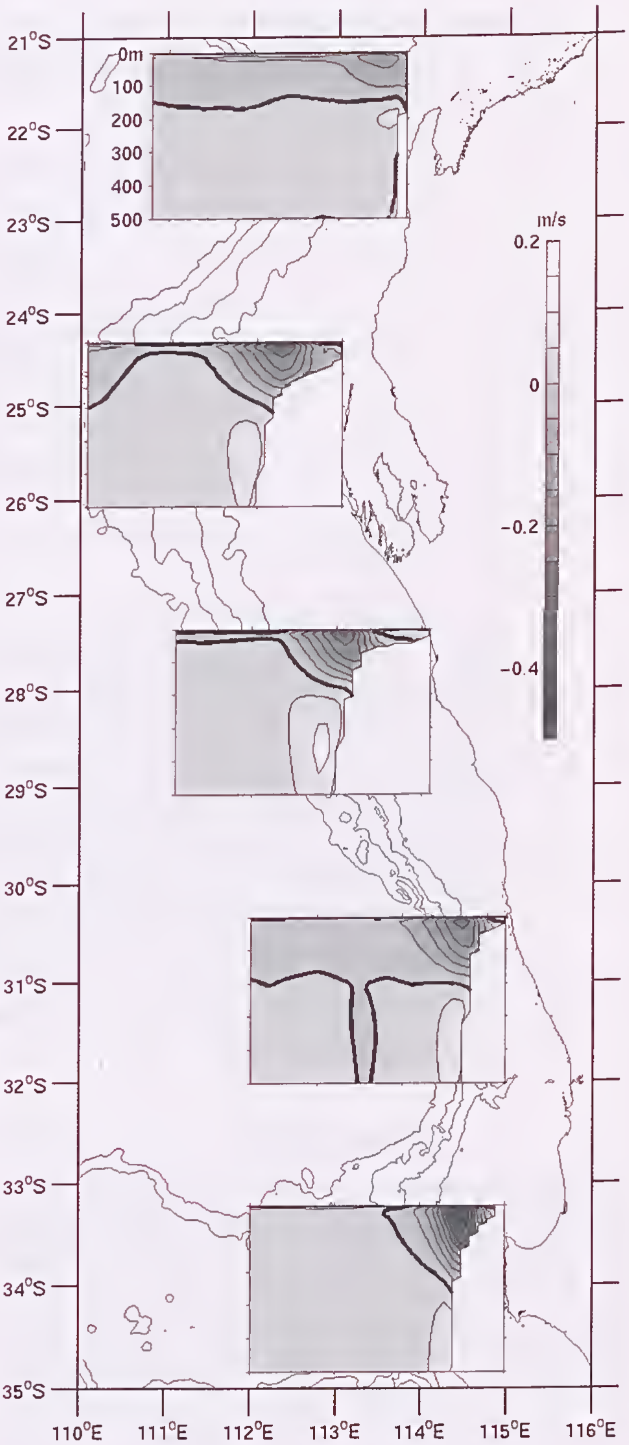


Figure 2. Mean meridional velocities at 22°, 25°, 28°, 31°, and 34°S in the upper ocean (0–500m) along the west coast of WA derived from the Ocean Forecast Australian Model (OFAM) 12-year simulation (Schiller *et al.* 2008).

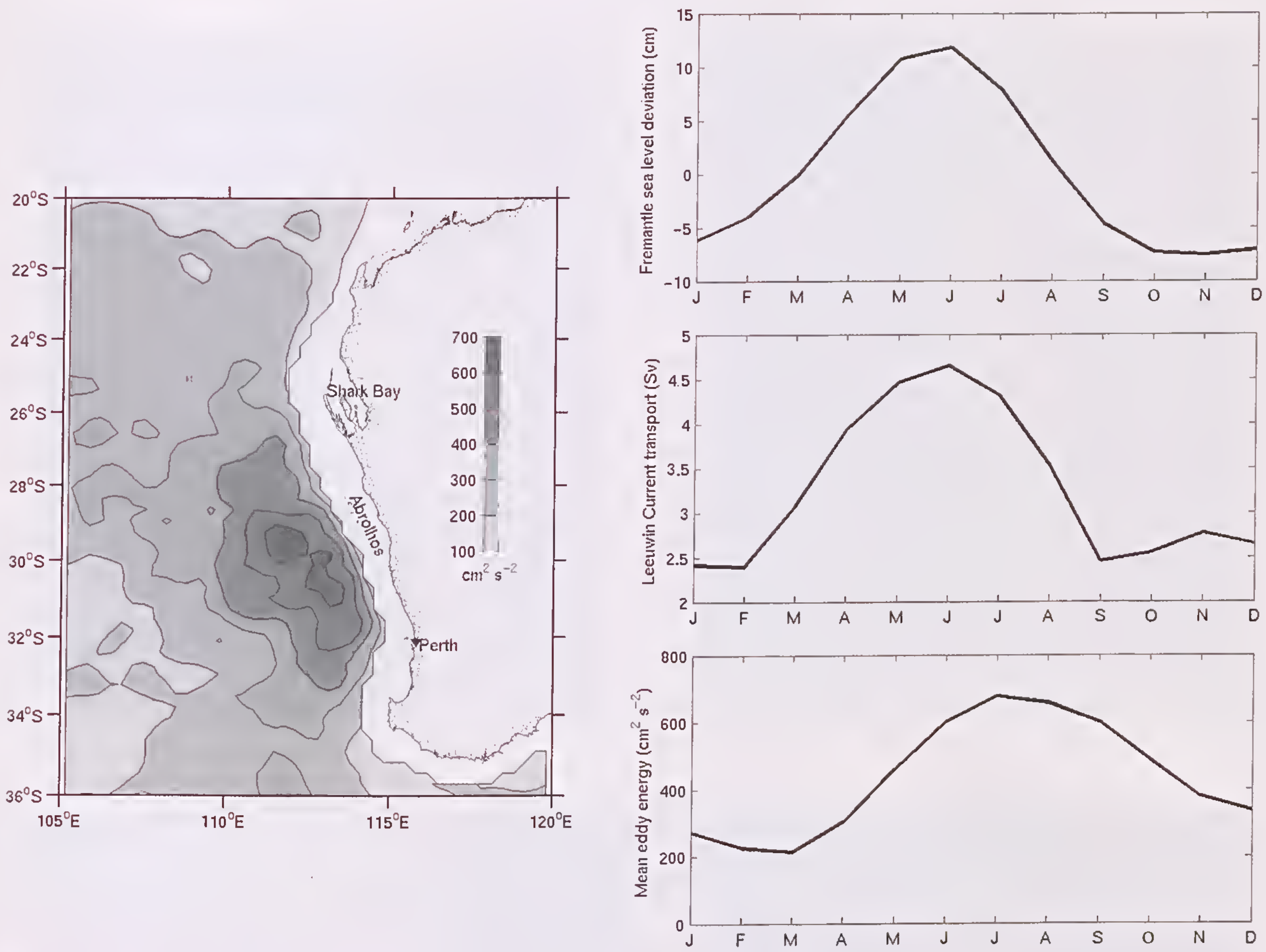


Figure 3. Long-term mean surface eddy kinetic energy derived from satellite altimeter data (left panel). The right panels (from top to bottom) are seasonal cycle of the Fremantle sea level, Leeuwin Current transport (Geostrophic & Ekman), and surface eddy kinetic energy between Abrolhos and Perth.

Different physical processes dominate the dynamic balances of the LC at different latitudes (Feng *et al.* 2005): north of Abrolhos, there is a balance between the southward pressure gradient and the northward wind stress; while south of Abrolhos, the pressure gradient is stronger and the alongshore wind stress is weaker so that the current is highly unstable and generates a strong mesoscale eddy field. South of Abrolhos, the Reynolds stress exerted by the eddy field is more important than the wind stress in balancing the southward pressure gradient (Figure 3; Feng *et al.* 2005). The LC eddies are important in the offshore transport of the momentum and heat from the LC (Fang & Morrow 2003; Feng *et al.* 2005; Domingues *et al.* 2006). On the seasonal cycle, the LC eddy field is strong during the austral winter and weak during the austral summer, such that the peak eddy energy occurs about 1 month later (July) compared to that of the peak LC transport (Figure 3). This would be expected since the eddy field draws its energy from the instability of the LC.

The ENSO related upper ocean variations propagate poleward as coastal Kelvin waves along the northwest to west WA coasts (Meyers 1996; Feng *et al.* 2003). The waves transmit high coastal sea levels (deep thermocline) and induce strong LC transports (4.2 Sv) during the La Niña years, and transmit low sea levels (shallow thermocline) and induce weak LC transports (3 Sv) during the El Niño years (Feng *et al.* 2003). A significant linear relationship between the Fremantle sea level and the volume transport of the LC across 32°S on the annual and interannual time scales can be derived. There is also a strong association between ENSO and the altimeter derived eddy energetics, $\frac{1}{2}(u^2+v^2)$, averaged between Abrolhos and Perth (Figure 4). Strong eddy energetics occurred during the La Niña years, *e.g.*, 1996, 1999, and 2000, while weak LC eddy energetics were observed during the El Nino years, *e.g.*, 1994, 1997, and 2002. During 1993–2006, the linear correlation between the annual mean Southern Oscillation Index (SOI) and the eddy energy is 0.94, demonstrating the strong sensitivity of the LC system to ENSO.

Another important feature of the physical environment in the LC is the strong surface heat loss along the southward flowing warm current. The heat loss is mostly due to the evaporative cooling (latent heat flux) when warm sea surface temperature in the LC meets the cold air temperature in the south and the frequent occurrence of winter storms originated from the Southern

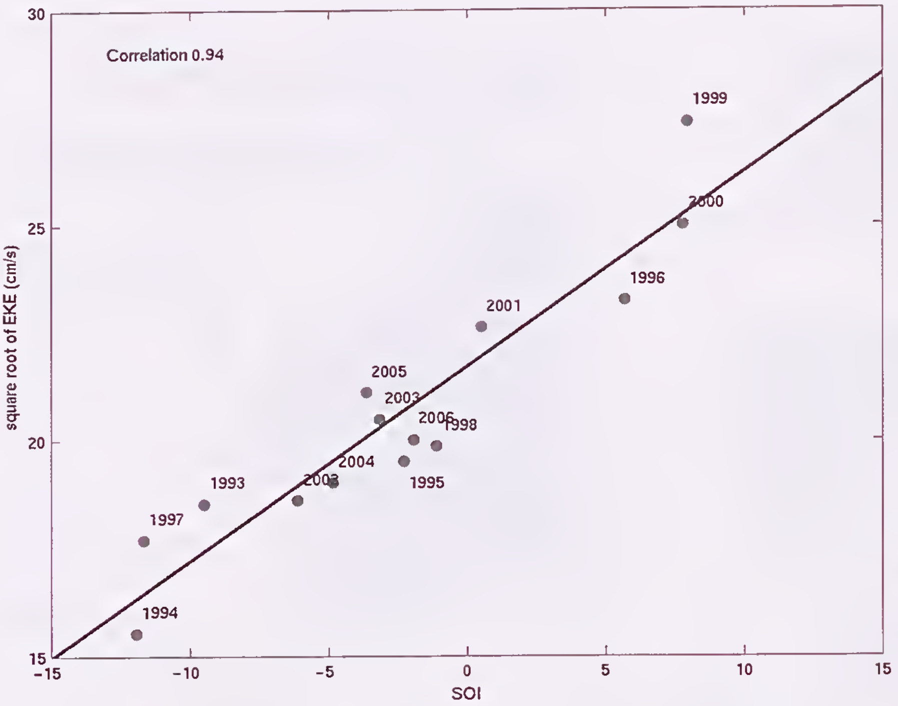
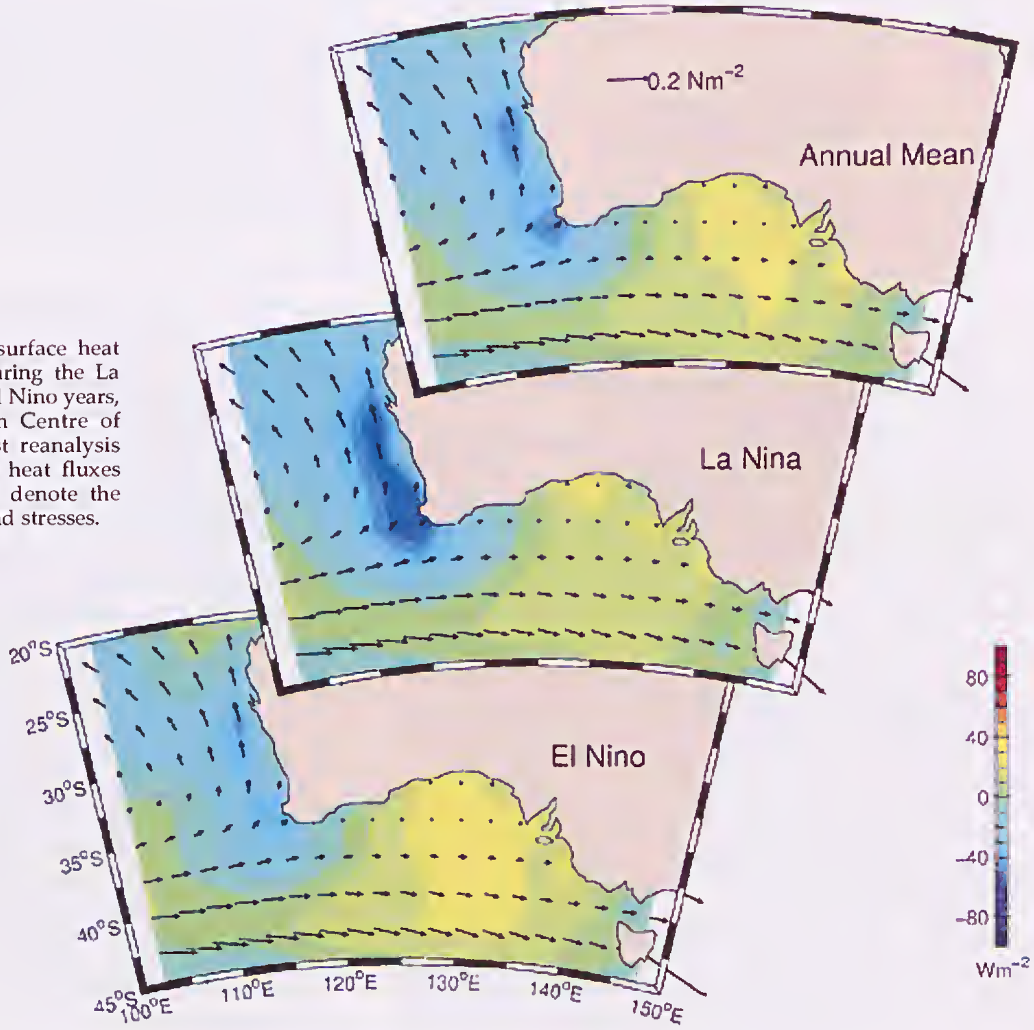


Figure 4. Relationship between annual mean Southern Oscillation Index (SOI) and the square root of the altimeter derived surface eddy kinetic energy (EKE) between Abrolhos and Perth ($R^2 = 0.88$).

Figure 5. Average net sea surface heat fluxes, during 1957-2002, during the La Nina years, and during the El Nino years, derived from the European Centre of Mid-range Weather Forecast reanalysis product. Positive fluxes are heat fluxes into the ocean. The arrows denote the composites of the surface wind stresses.



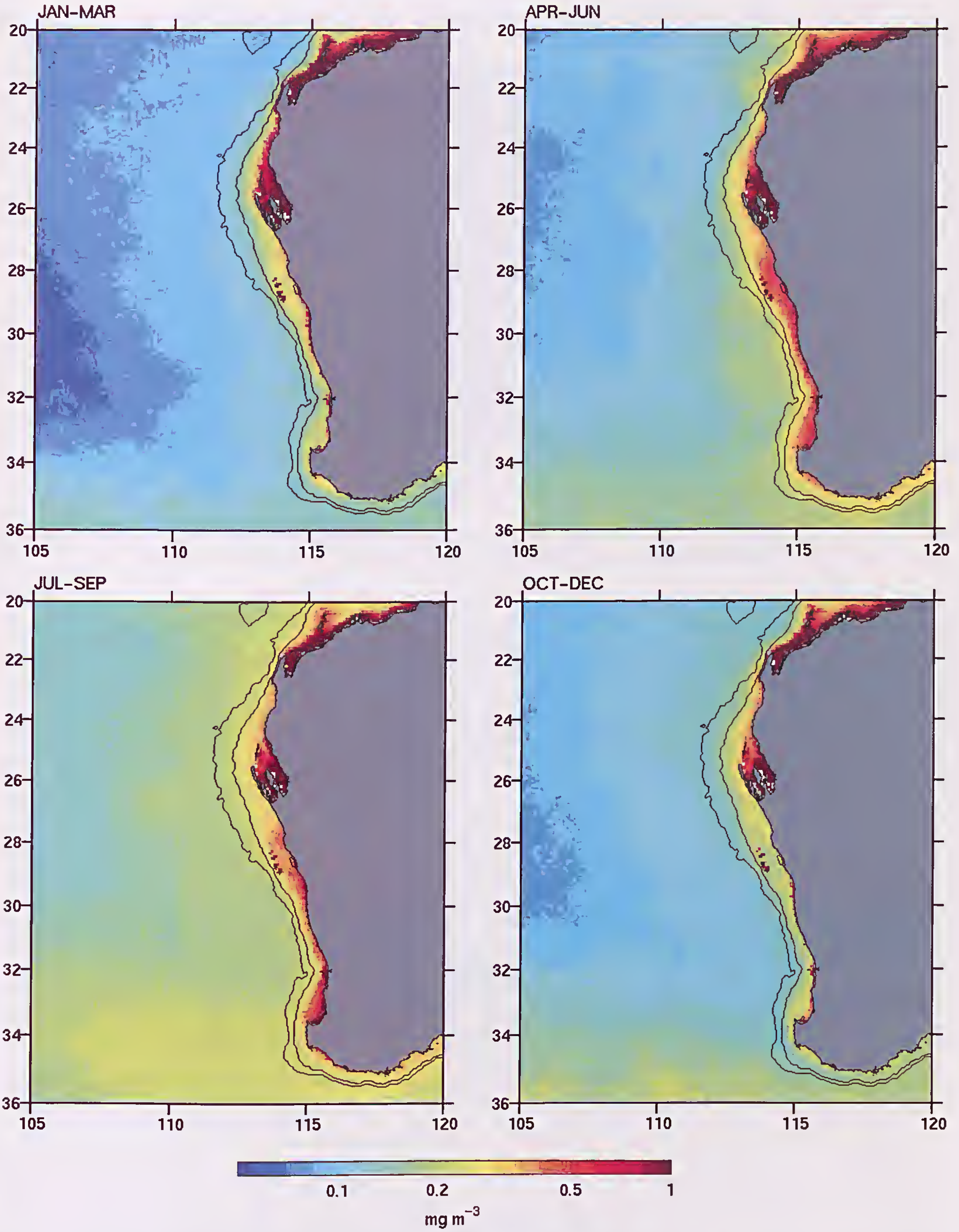


Figure 6. Seasonally-averaged sea surface chlorophyll *a* concentrations in the southeast Indian Ocean calculated from SeaWIFS monthly climatology data (1997–2007). The bottom bathymetry is denoted for the 50, 200, and 1000 m isobaths (adapted from Feng & Wild-Allen 2009).

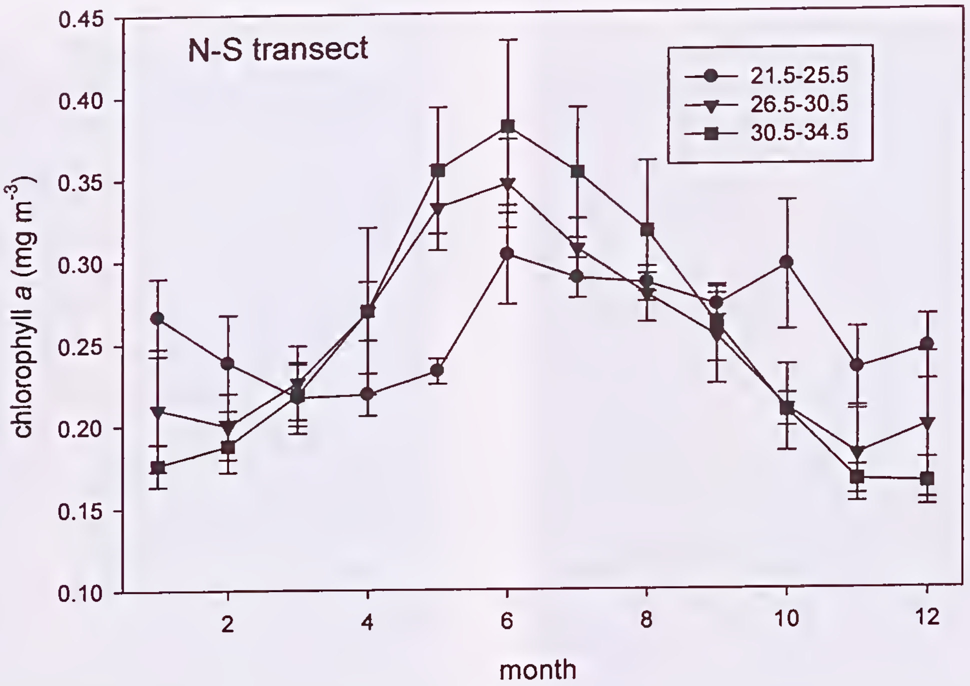


Figure 7. Monthly climatology of sea surface chlorophyll *a* concentrations averaged over three latitude bands on the shelf (approximately in the 100 and 1000 m depth range) off WA, derived from the 1997–2007 SeaWiFS ocean colour satellite data.

Ocean. The evaporative cooling is strong during austral winter, when the LC transport is strong. There are also consistent ENSO-related interannual variations in the surface heat loss – the heat loss is stronger during the La Nina years and weaker during the El Nino years (Figure 5). Surface cooling can induce strong vertical mixing which affects stratification in the water column and thus is important in nutrient cycling in the mixed layer of the LC (Greenwood *et al.* 2007).

Satellite measurement of chlorophyll *a* concentration

The launch of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite in the late 1990s has provided measurements of upper ocean chlorophyll *a* concentration with 30% accuracy (Bailey & Werdell 2006). The SeaWiFS data have been used to quantify the seasonal variations of surface phytoplankton biomass in the LC system (Figure 6 Feng *et al.* 2007; Moore *et al.* 2007). The accuracy of the satellite data also allows us to explore the interannual variability.

In the oligotrophic marine environment off the west coast of WA, there are low upper ocean chlorophyll *a* concentrations compared to other eastern boundary current systems (with typical value of ~1 mg m^{-3}; http://oceancolor.gsfc.nasa.gov/cgi/climatologies.pl). There has been a recent discovery of late-autumn to early-winter chlorophyll *a* enhancement in the LC system south of Abrolhos from *in situ* observations (Koslow *et al.* 2008), which is also captured by the satellite measurements (Lourey *et al.* 2006; Feng *et al.* 2007; Moore *et al.* 2007). Averaged over the shelf (approximately in the 50–1000 m depth range), consistent late-autumn to early-winter (May–June) peaks of upper ocean chlorophyll *a* concentrations are observed south of Abrolhos, with peak values of about 0.4 mg m^{-3} (Figures 6 and 7). Offshore of the LC and within about 500 km off the coast, late-winter (July–September) phytoplankton enhancements are generally observed (Figure 6), with winter values of about 0.2–0.3 mg m^{-3}. Further offshore in the oligotrophic, subtropical open-ocean, the chlorophyll *a* concentration is very low and there is a winter peak of less than 0.2 mg m^{-3}. The September–October chlorophyll *a* peaks south of 32°S are likely due to the northward migration of the subtropical front, with peak values of about 0.3 mg m^{-3} (Figure 6). On the continental shelf north of Shark Bay, there is the summer (January) chlorophyll *a* peak (Figure 6), which is driven by upwelling favourable winds (Hanson *et al.* 2005a). The broad winter (June–October) peak in Figure 7 is likely due to that the box for average is relatively large so that winter peak in the offshore region may dominate the average. Most of the seasonal cycles are significant compared with the 30% accuracy range.

There are detectable interannual variations in the upper ocean chlorophyll *a* concentrations on the continental shelf off the west coast (Figure 8a). North of 28°S (Abrolhos), positive chlorophyll *a* concentration anomalies are observed during 2000–2001, and 2004–2006, while there are negative anomalies during 1999 and 2002. The variations south of 28°S tend to be correlated with Southern Oscillation Index, with positive anomalies in 1999–2000 and 2006 and negative anomalies in 1997 (not shown), and 2002–2004 (Figure 8b). These north-south differences suggest that more than one physical factor influences the interannual variations in chlorophyll *a* biomass and ocean production along the west coast. Note that averaged over the spatial domain of the LC the

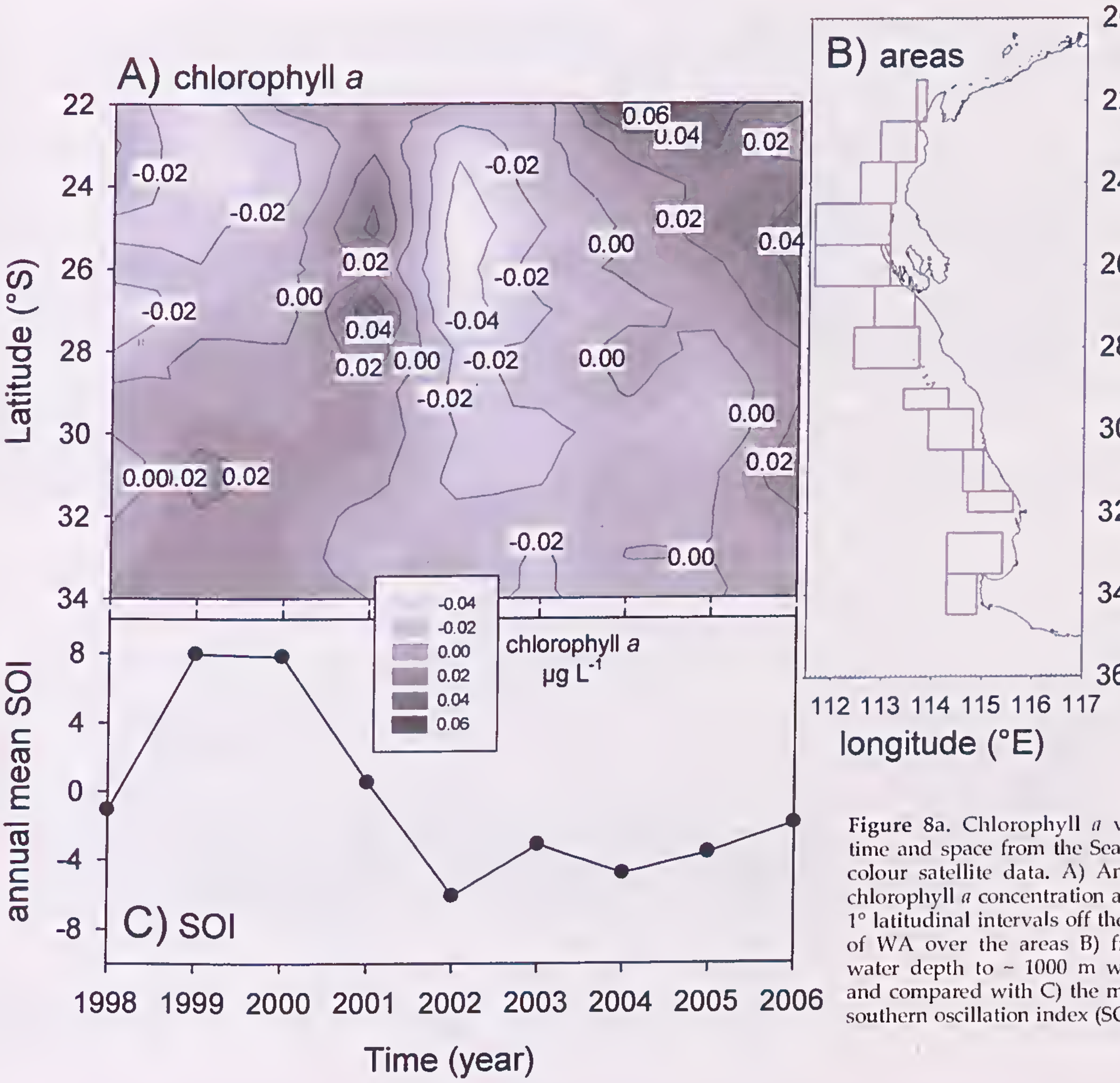


Figure 8a. Chlorophyll *a* variation in time and space from the SeaWiFs ocean colour satellite data. A) Annual mean chlorophyll *a* concentration anomalies at 1° latitudinal intervals off the west coast of WA over the areas B) from ~ 50m water depth to ~ 1000 m water depth, and compared with C) the mean annual southern oscillation index (SOI).

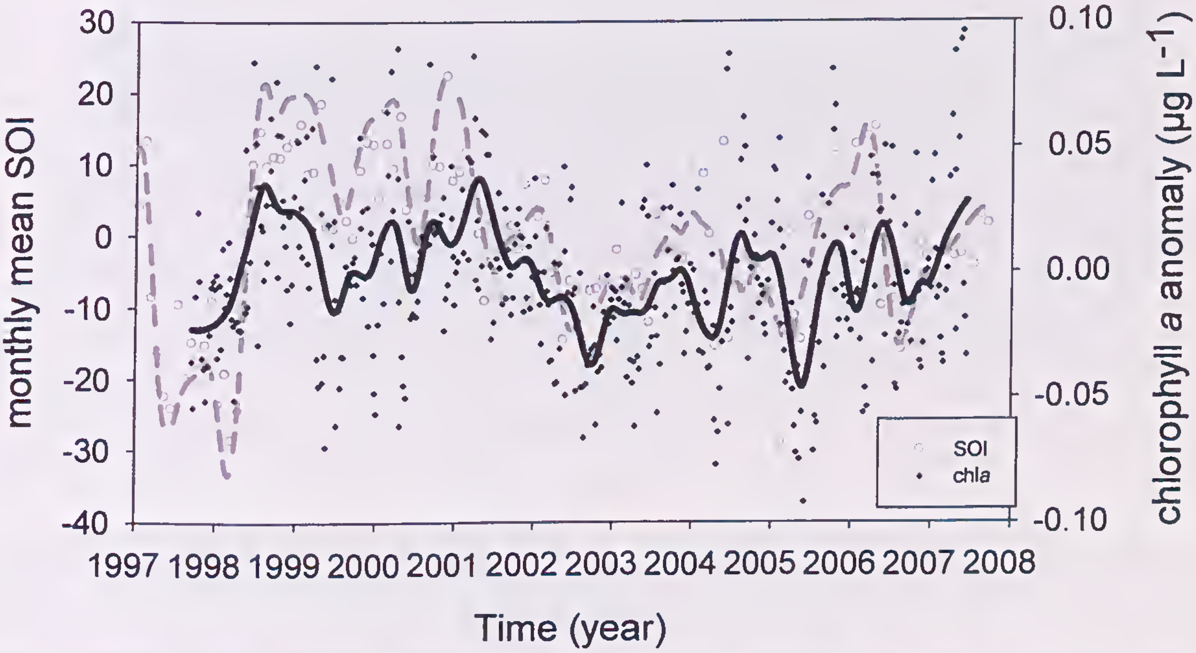


Figure 8b. Time series of 8-day chlorophyll *a* anomalies from SeaWiFs ocean colour satellite data over the area 29 to 31°S and 113.5 to 114.5 °E off the west coast of WA. The monthly chlorophyll *a* anomaly (solid line) could be approximated by a linear function of monthly SOI (dashed line); $r^2 = 0.135$, $P < 0.001$.

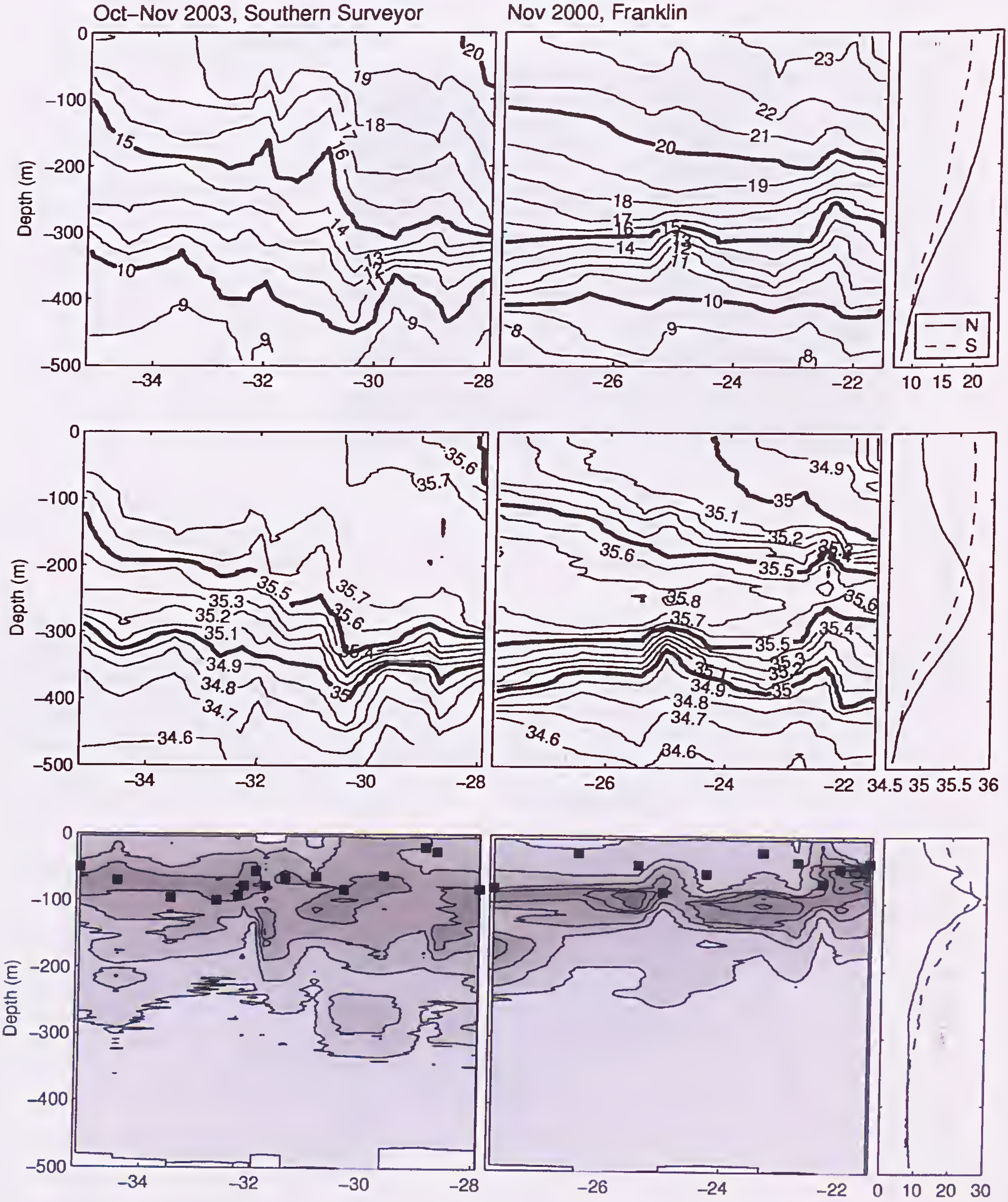


Figure 9a. (top panel) Temperature, (middle panel) salinity and (lower panel) fluorescence readings collected with CTD (conductivity-temperature-depth) sensors along the 500 isobath during October–November 2000 and 2003. The unit for temperature is °C and the darker shadings denote higher fluorescence readings. The solid squares in the fluorescence panels denote the CTD station and the mixed layer depth. The averaged profiles north (solid) and south (dashed) of 28°S are displayed to the right of each panel.

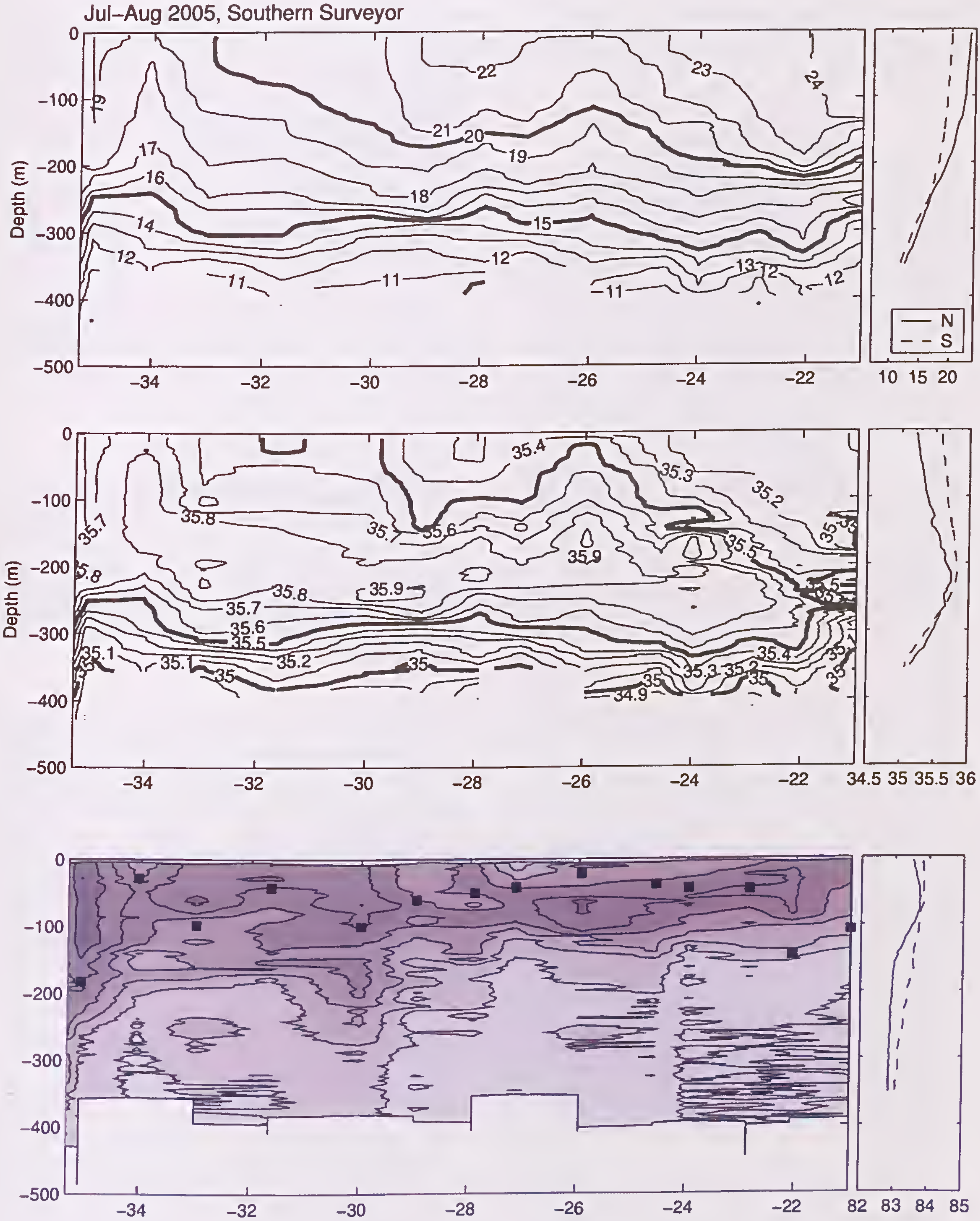


Figure 9b. same as Figure 9a except for the July-August 2005 Southern Surveyor cruise.

annual chlorophyll *a* anomalies is a small fraction (less than 30%) of the total standing stocks (Figure 8a), so that precautions should be taken in interpreting the interannual variations.

In situ observations

In recent years, a number multi-disciplinary research cruises have been carried in the LC system off the west coast of WA. In combination with satellite observations, the cruise data have been used to understand the nutrient dynamics off the coast, especially the coastal upwelling off the NW Cape and the role of mesoscale eddies (Morrow *et al.* 2003; Hanson *et al.* 2005a, 2005b; Waite *et al.* 2007; Thompson *et al.* 2007; Koslow *et al.* 2008). In this section, we use two north-south hydrographic sections along the continental shelf break during the two opposite seasons (spring/summer and autumn/winter) to highlight the north-south and seasonal variations of the biophysical properties along the west coast of WA.

From alongshore (500 m isobath) sections during the austral spring (a composite from the R/V *Franklin* cruise in November 2000 and the R/V *Southern Surveyor* cruise in late October–November 2003), there are general decreasing trend of temperature and increasing trend of salinity in the upper 200 m (the LC) from north to south (Figure 9a). Air-sea fluxes and exchanges with subtropical water masses modify the LC waters when the current flows southward. North of Abrolhos, both temperature and salinity stratifications contribute to produce a relatively strong and shallow thermocline (<100 m). Salinity maximum (>35.7 psu) subtropical surface waters formed in the mid-latitude due to excessive evaporation are subducted to about 200 m depth north of Abrolhos (Figure 9a), which further strengthens the density stratification in the north. The subducted waters are partly entrained in the LC and partly entrained in the northward flowing Leeuwin Undercurrent (Domingues *et al.* 2007). In the south, the thermocline is relatively deep, likely due to the convergence of the LC (Figure 9a). The salinity stratification partly compensates the temperature stratification so that the density stratification in the upper ocean is relatively weak. The diffused thermocline is also likely due to the stronger LC eddy activity in the south. Subduction of the South Indian Ocean Central Water may also contribute (*e.g.*, Woo & Pattiaratchi 2008).

Inferred from fluorescence data, there are well-defined deep chlorophyll (biomass) maximum (DCM) layers north of Abrolhos Islands in late spring (Figure 9a). The DCM is at about 50 m depth off Ningaloo (22°S), where the wind-driven upwelling may be important (Hanson *et al.* 2005a), and at about 100 m depth in other shelf areas in the north. South of Abrolhos, the DCM layers still exist but are more diffused than those in the north, as shown in the average profiles north and south of Abrolhos.

There are similar decreasing trend in temperature and increasing trend in salinity from north to south in the upper 200 m along the shelf break (400 m) during the July–August 2005 (Figure 9b), except that the salinity maximum waters are no longer exposed to the sea surface, likely due to the stronger LC in winter that brings less salty tropical waters residing on the top of the local water mass. There also tends to be stronger mesoscale variability along the pathway of the LC, compared to spring, such as there are upwelling centres near 26°S and 34°S and downwelling centres near 22°S and 29°S. The upper ocean water column is less stratified compared to summer, likely due to the combined actions of the mesoscale eddies and mixing driven by the surface heat loss.

In July–August 2005, the DCM south of Abrolhos no longer exists and there is a near surface chlorophyll *a* maximum (Figure 9b). In the north, the DCM layers are slightly shallower than 100 m and are more closely linked to the mixed layer depths.

There are no suitable *in situ* observations that can well resolve the interannual variations of the biological properties in the LC system. Long term *in situ* monitoring of the biophysical properties in the LC is planned as part of the national Integrated Marine Observing System.

Nutrient dynamics

In the context of climate-driven ocean variability, we next consider the primary physical factors likely to influence nutrient fluxes, and thus primary production, in the LC. The main questions to be addressed are: what are the key processes that cause differences in the seasonal cycle of chlorophyll *a* concentrations north and south of the Abrolhos Islands? What are the drivers of the interannual variability of biogeochemical cycling along this coast?

Seasonal cycle

While north of Abrolhos enhanced nutrient concentrations are observed during the episodic upwelling events in summer (Hanson *et al.* 2005a), off the lower west coast, enhanced concentrations of dissolved nitrate and silicate have been observed during the austral autumn-winter, when the LC and its eddy field are strong and the continental shelf off the lower west coast of WA is flooded with the LC waters (Johannes *et al.* 1994; Thompson & Waite 2003; Hanson *et al.* 2005b; Koslow *et al.* 2008). This highlights strong seasonal differences in the LC influence north and south of Abrolhos, and therefore potentially the physical mechanisms controlling nutrient supply and primary production.

Mechanism 1 – Meridional erosion of seasonal thermocline drives nutrient injection into surface layers.

In the ITF region and north of Australia, the thermocline and nitrocline are relatively shallow, due to both excessive heat and freshwater inputs at the sea surface. As the tropical waters move south to join the LC and enter regions with a progressively deeper seasonal thermocline (Domingues 2006), the thermocline is eroded by vertical mixing and nutrients immediately below the thermocline could be mixed into the surface layer (Figure 10). South of Abrolhos, the DCM tends to be shallower than the nitrocline depth during the austral winter (Figures 9b and 11), likely due to less stratification and stronger vertical mixing.

This mechanism would clearly have a seasonal component, and be most likely to occur during periods of

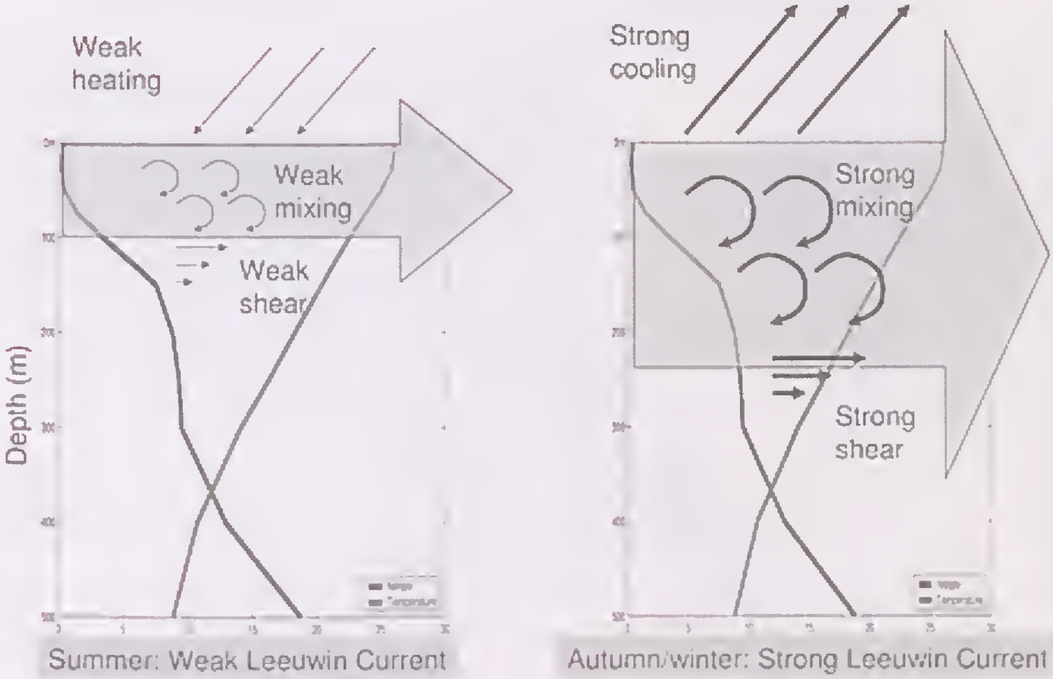


Figure 10. Schematic on how the erosion of the thermocline could bring nitrate into the euphotic layer in the LC system. The left panel is the summer condition when the LC is weak and the right panel is for the autumn/winter condition when the LC is strong. The schematic may also be applied to the difference between the El Niño and La Niña years. The vertical profiles of temperature (light line, unit: °C) and nitrate (dark line, unit: mg m^{-3}) are for the typical tropical waters near the source region of the LC.

accelerating LC (*i.e.*, March – June) and/or significant overall surface cooling, which could continue well into winter (Figure 10). Once this nutrient injection was exhausted, the vertical structure would likely revert to a more typical "tropical structure" (Cullen 1982) where diffusion of nutrients from below balances light from above, resulting in the formation of DCM (Figure 9a). This mechanism is considered to be one of the key processes for nutrient injection for the late autumn to early winter chlorophyll enhancement in the LC.

Mechanism 2 – The lifting/dropping of the nitrocline can increase/decrease primary production.

North of Abrolhos, the DCM is below the mixed layer depth (Figure 9), indicating that the DCM develops due to typical tropical conditions (Cullen 1982). The DCM depth is strongly correlated with the nitrocline depth (Figure 11), and there tends to be greater production when or where the DCM and nitrocline depths are shallower (Hanson *et al.* 2005a), indicating the sensitivity of upper ocean production to vertical movement of the thermocline (nitrocline) depth. This mechanism is responsible for the summer chlorophyll peaks north of Abrolhos.

Mechanism 3 – Both the horizontal and vertical advection related the eddy activities are important in enhancing ocean production in the LC system.

The presence of eddies generally contributes to enhance the biological productivity. Jenkins (1988), and later McGillicuddy & Robinson (1997) propose that in the oligotrophic Sargasso Sea, the time-varying eddy field may supply the required nutrients to sustain the observed primary production in the nutrient depleted gyre, due to eddy upwelling mechanism.

In the LC region, a Southern Surveyor section, which transverses an anticyclonic eddy and a cyclonic eddy, captures enhanced chlorophyll *a* signatures in both types of eddies (Figure 12). There tended to be enhanced primary production in mesoscale eddies, especially in the warm-core eddies associated with the LC (Waite *et al.* 2007; Feng *et al.* 2007). The nitrocline depth far exceeds the DCM depth in the eddy field compared with those in the LC (Figure 11), indicating that eddy activity may have enhanced the mixing of water masses. Another important role of eddy activity to regional biogeochemistry is their ability to transport properties horizontally across streamlines of the mean flow (Feng *et al.* 2007). In addition, the entrainment of productive waters from the continental shelf during the eddy formation (Greenwood *et al.* 2007; Paterson *et al.* 2008) results in the transport of particulate nutrients offshore.

Mechanism 4 – In situ nitrification can increase localized production.

There is possibly anecdotal evidence that nitrification may be occurring below the mixed layer depth in the anticyclonic LC eddies (Paterson *et al.* 2008).

Mechanism 5 – Benthic-pelagic coupling may be an important process on the seasonal cycle

From a simple nitrogen budget for the west coast of WA (Feng & Wild-Allen 2009), the benthic input may

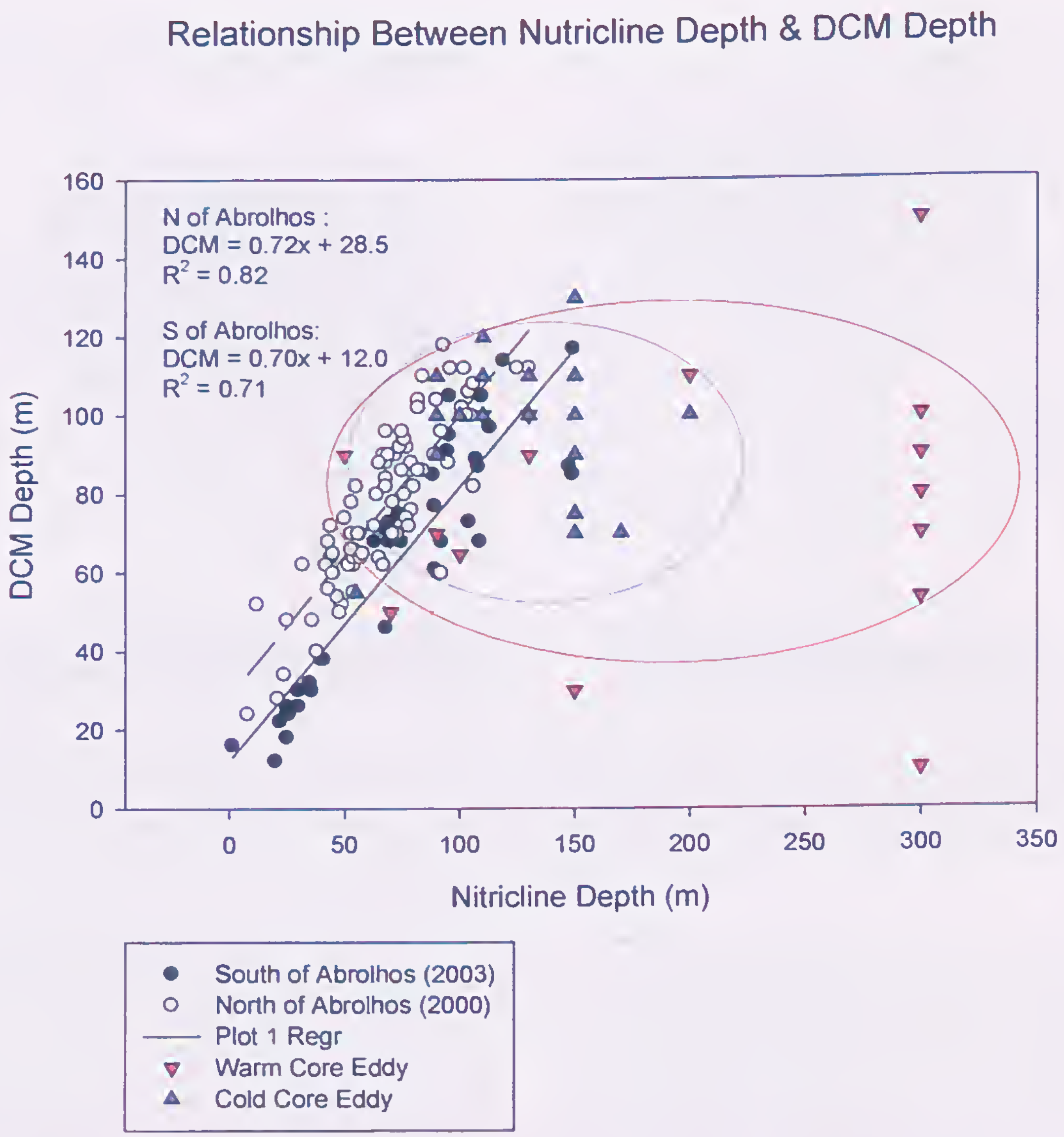


Figure 11. Relationships between the nitrocline depth and the deep chlorophyll maximum depth north and south of Abrolhos Islands along the LC, observed in November 2000 and October-November 2003, respectively. The straight lines are linear regressions for the two regions. The relationships in two offshore mesoscale eddies in October 2003 are also shown as triangles and are highlighted with elliptical shapes.

provide a significant portion of the nitrogen required to support the annual primary production on the continental shelf. Note that the benthic re-supply of nutrient to the water column is driven by storms and swells, which is coincident with strong onshore winds during the austral autumn-winter.

In summary, there are a few important physical and biological factors that potentially influence the seasonal cycle of the nutrient dynamics in the LC and on the shelf. Some factors have large-scale impacts and can affect the whole LC region, such as the air-sea heat flux (Figure 5). Some factors have different impacts on the nutrient dynamics north and south of Abrolhos, such as wind-driven upwelling being more effective north of Abrolhos due the shallow nitrocline, while the LC and eddy advection being more effective south of Abrolhos.

Interannual variations

During the La Niña years, the stronger LC is linked with a deeper thermocline (nitrocline) depth off the shelf edge so that the wind-driven upwelling is less effective in bringing deep nutrient onto the shelf, likely resulting in reduced summer production north of Abrolhos (Furnas 2007). The opposite would occur during the El Niño years.

In the south, with the assistance of the stronger eddy field and greater surface heat loss, the stronger LC during the La Niña years likely leads to stronger thermocline erosion and higher nutrient flux into the upper ocean, so that it is likely that the primary production is enhanced due to the increased LC strength. The opposite would likely occur during an El Niño year. Thus, in this region the primary production may not

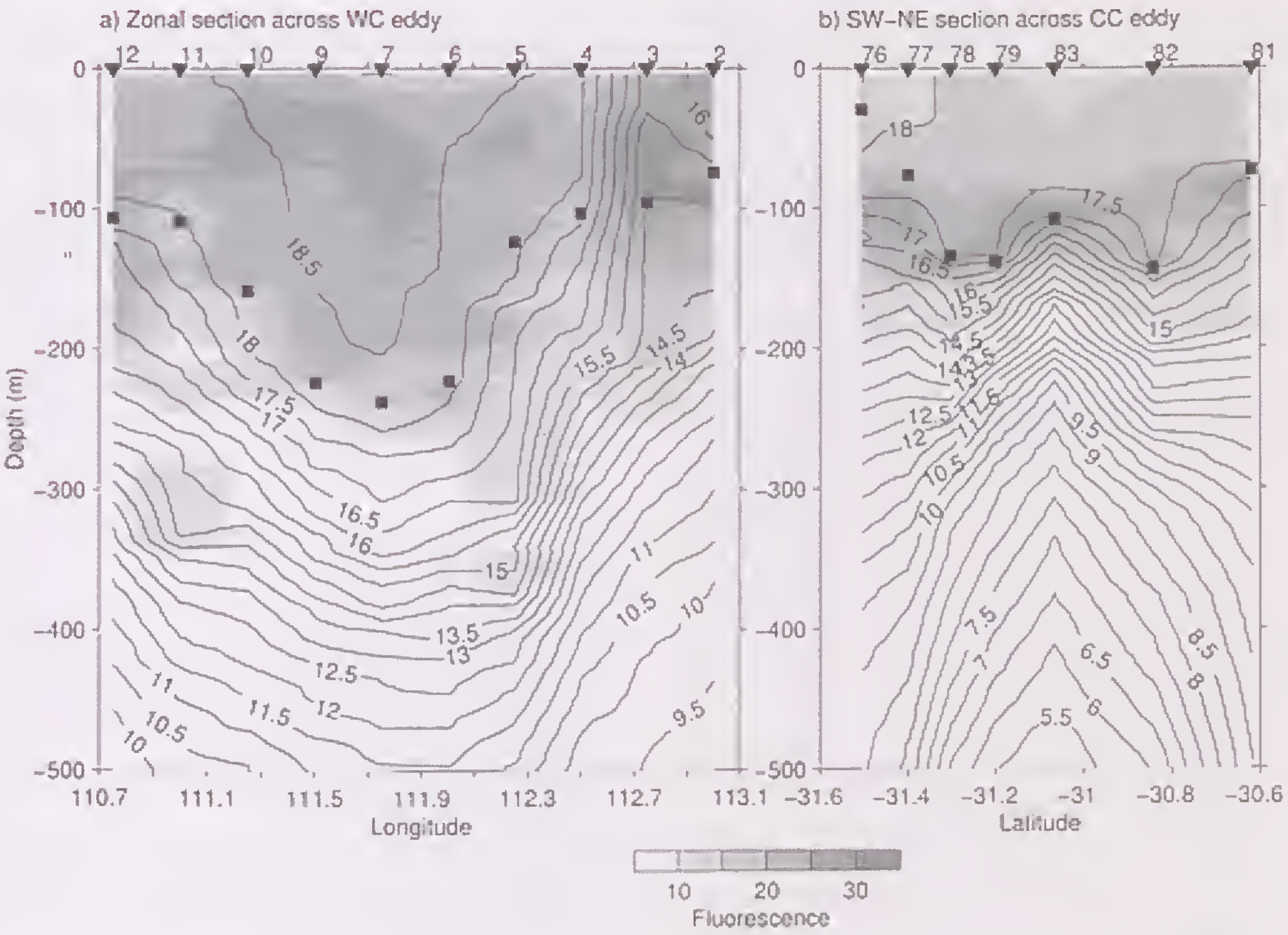


Figure 12. Vertical temperature structures along two transects across a warm-core (WC) eddy (a) and a cold-core (CC) eddy (b) from Feng *et al.* (2007).The shadings denote the fluorescence measurements and the solid squares denote the depth of the mixed layer. The station numbers of the CTD casts are denoted on the tops of the panels.

follow the global trend in response to ENSO (Behrenfeld *et al.* 2006), *e.g.*, there is a cooling trend of sea surface temperature (SST) during 1999–2004 off the lower west coast of WA (Pearce & Feng 2007), while there is a decreasing trend in chlorophyll *a* biomass over the same period (Figure 8).

Climate change and potential impacts

In the past 50 years, SST off the west coast, especially the lower west coast, of Australia, is warmed up faster than the average trend of the global ocean (Pearce & Feng 2007). From climate model simulations, it is suggested that in a warming climate, mean state in the tropical Pacific evolves towards a more El Niño-like condition, with reduced trade winds and reduced thermocline tilting (IPCC, 2007). The reduced thermocline tilting has produced a shallow thermocline anomaly in the Eastern Indian Ocean as well as along the west coast of WA (Wainwright *et al.* 2008). The observed trends in the tropical Pacific and Eastern Indian Ocean have shown that the Indonesian Throughflow may have reduced its strength by 20% in terms of volume transport. The shallowing of thermocline in the Eastern Indian Ocean implies a reduction of the pressure gradient that drives the LC, and hence a reduction in the LC transport (Feng *et al.* manuscript in preparation). In regional climate, there has been a significant decrease of rainfall in the southwest WA region during the recent decades, due to fewer winter storms arriving at the coast (IOCI 2002). The reductions of the LC and the winter storms are expected to reduce nutrient inputs into the upper ocean south of Abrolhos. North of Abrolhos, where the ocean productivity is more sensitive to the depth of the nitrocline, the ocean production is likely to increase with a weakening LC. In addition, with the global warming the surface layer of the ocean becomes lighter and less likely to mix with the colder, denser water below, so that in principle, primary productivity would be reduced in a general sense (Behrenfeld *et al.* 2006).

To accurately predict these effects, we need to have a combined assessment of the effects of the global warming, changes in regional circulation, and changes in the regional air-sea heat fluxes. This will be achieved through long-term monitoring of the shelf environment and climate model downscaling for the LC system. Further research on the biogeochemical responses of the LC system to climate variability and climate change is necessary to underpin the long term management of the marine resources in this region.

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The Leeuwin Current south of Western Australia

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Abstract

Two centuries ago Matthew Flinders detected an eastward-flowing current above the continental slope south of WA. A succession of advances in instrumentation, particularly since World War II, has led to a description of that current, the Leeuwin Current: Its tropical low salinity and subtropical high salinity waters arrive at Cape Leeuwin from the north and west in austral autumn and its leading edge progresses eastward at about 20 km day^{-1} into the low salinity subantarctic regime south of WA. The Leeuwin Current meanders on and off the continental shelf as far as the Recherche Archipelago. Off the shelf, its speeds can be as high as 1.8 ms^{-1} and its influence reaches down to 250 m. Beyond the Archipelago, in the Great Australian Bight, it is weaker, with speeds of about 0.3–0.5 ms^{-1} near the shelf edge. The region westward from the Archipelago is rich in eddies that interact with and distort the Leeuwin Current: anticyclonic eddies divert it out to sea and take on some of its waters; cyclonic eddies accelerate it on their northern sides. The current speeds in anticyclonic eddies decrease very little from the surface down to 250–300 m depth. A current meter mooring on the shelf near the Recherche Archipelago indicated that the Leeuwin Current was present most of the time from December 2001 to August 2002. The shelf currents were strongly influenced by winds from passing weather patterns. The results from recent numerical modeling show good agreement with the observations and show subsurface trajectories that would be difficult to capture by observation.

Keywords: Leeuwin Current, Western Australia, salinity, temperature, historical account

Introduction

The Leeuwin Current (LC) is a well-documented current system, of varying intensity, salinity and temperature, deriving in part from extra-Australian sources, and occurring off the coast of Western Australia (Waite *et al.* 2007). In Australian waters the maximum speeds attained by the narrow Leeuwin Current above the upper continental slope of southern Western Australia (WA), are second only to those of the broader East Australian Current, namely ~1.8 ms^{-1} versus 2.5 ms^{-1} (we exclude near shore tidal currents in northern Australia). The LC brings waters of both tropical and subtropical origin around Cape Leeuwin and thence eastward into the subantarctic regime south of WA. This sub-Antarctic regime is rich in eddies that interact with and distort the LC: anti-cyclonic eddies divert it out to sea and take on some of its waters, strengthening in the process; cyclonic eddies accelerate it on their northern sides. The region enjoys considerable biodiversity as a result of the sub-Antarctic, subtropical and tropical waters bringing to it different marine flora and fauna.

In this paper we examine historical work on the currents south of WA as techniques evolved from sailing ship observations in the early 19th century through to the shipboard electrical and acoustical measurements of water properties and current profiles and the satellite measurements of sea surface temperature in the 1980s. Then we examine both published and unpublished observations from 1994 onwards, 1994 being a special year in that there were three voyages by the research vessel *Franklin* – albeit uncoordinated and with vastly different aims – when, for the first time, satellites provided sea surface height measurements. With the near-continuous maps of sea surface topography from satellites one could follow the evolution of currents and eddies and more effectively interpret the sporadic *in situ* ship measurements. Then we examine current records for a nine-month period (December 2001 to August 2002) from on the continental shelf near the Recherche Archipelago. Finally, the results from a numerical model are examined, and they show, among other things, the arrival in autumn of the LC waters south of WA, in agreement with observations.

History

Early 19th century to the 1970s

The charts of Flinders (1814) for his voyages south of WA in December 1801 and May 1803 contain information on the geography of the coast and hinterland, on depths, bottom types, the weather encountered, and the currents experienced. Near the continental shelf between Cape Leeuwin and present-day Albany (118°E), the current was eastward at 1 ¼ knots (about 0.6 ms^{-1}). Farther eastward on the continental shelf of the Great Australian Bight, Flinders reported that *"the water does not seem to run in any constant direction, for is moved according as the* *wind may happen to blow. This was found by admiral D'Entrecasteaux; and is conformable to my experience..."* Flinders described a line "from the north-eastern isles of the Archipelago of the Recherche to Cape Northumberland (near 140°E on the coast of South Australia), we shall have what will commonly be the northern boundary of the current." In other words, he felt that the current that was strong between Cape Leeuwin and Albany may have continued across the Great Australian Bight, but a long way offshore.

Halligan's (1921) remarkable chart of the ocean currents around Australia drew on the observations of, among others, Flinders, King, Wickham, Stokes and Ross – and referred to vessels such as *La Venus, Geographe,* Naturaliste and *Challenger.* The chart showed a warm Indian Ocean stream rounding Cape Leeuwin and flowing eastward. He said that the 62°F (~16.5°C) isotherm lay east-west across the Indian Ocean, but deviated southward near WA, being carried a maximum of 200 miles south of Cape Leeuwin in June. The subsurface temperature measurements from *Challenger* led Halligan to describe what we would now call the Leeuwin Undercurrent going *"as far north as Shark Bay, having dipped below the warm southerly drift".* Halligan mentioned a cold belt against the WA coast that was due to upwelling, which varied according to the strength and duration of the winds – a feature that we would now describe as the Capes Current (Gersbach *et al.* 1999).

Schott (1935) presented charts of ship drifts, temperature and salinity that suggested the flow of warm water around Cape Leeuwin and eastward towards the Great Australian Bight.

The influence of the Leeuwin Current south of WA is evident in the marine biology of the region: Wood (1954), through observations of subtropical dinoflagellates, postulated that a current flowed eastward from Cape Leeuwin to Tasmania and claimed that this was confirmed by "the finding of warm-water turtles on the west coast of Tasmania".

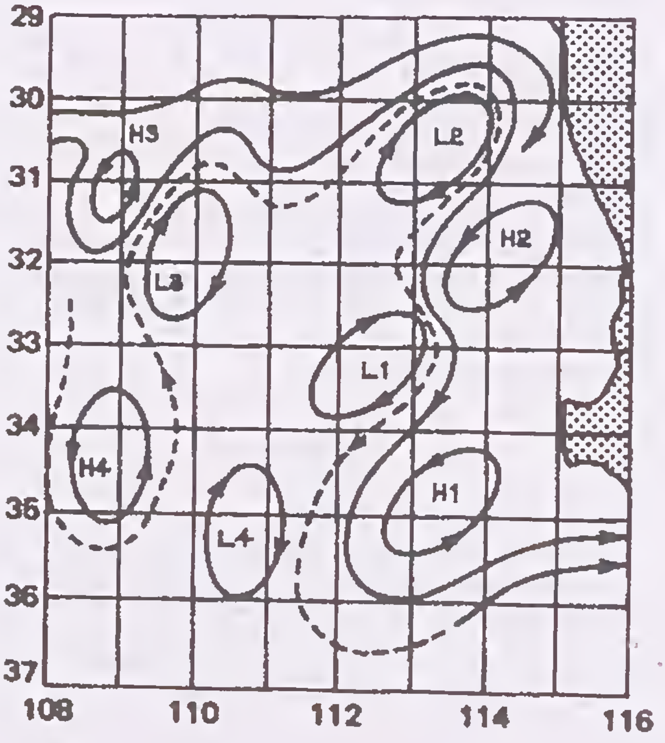

Figure 1. A schematic diagram from ship surveys of the mesoscale features west of WA (Andrews 1977).

Following World War II, Australia's small core of oceanographers used navy frigates for studies around the nation. Hamon's (1965) Nansen bottle observations ("hydrocasts") showed that there was a flow of relatively salty water from the central Indian Ocean towards WA at about 30°S. Andrews (1977) conducted near-synoptic three dimensional temperature mapping with expendable bathythermographs (XBTs), a first for Australian waters. The maps showed that Hamon's inflow was embedded in a field of cyclonic and anticyclonic eddies and that it turned southward at the continental shelf edge and then eastward at Cape Leeuwin, thus entering the study region for this paper (Figure 1).

Satellite tracked drifters in the 1970s

The technology for tracking drifters with satellites first became available in the early 1970s and soon after a dozen drifters built by CSIRO were released off WA. They were important in revealing the LC and prompted its naming. They showed that the LC not only flowed southward near the continental shelf edge to the Cape Leeuwin vicinity, but that it accelerated around the Cape and then flowed eastward at speeds up to 1.8 ms^{-1} towards the Great Australian Bight (Cresswell & Golding 1980). The current had small (~30 km) southward (anticyclonic) meanders separated by ~ 200 km. At the locations of the southward meanders there could be transient offshoots out to sea that took the drifters into cyclonic eddies, where they remained trapped for some weeks. In some instances, the drifter motions showed the cyclonic eddies to drift westward at about 7 km day^{-1}. The drifters decelerated when they entered the cool cyclonic eddies from the LC and accelerated when they re-entered it. The groundings of several drifters along the south coast suggested that the LC could spread in across the continental shelf. Some drifters came from the south to suggest that subantarctic waters were carried northward to interact with the LC.

Satellite sea surface temperature images in the 1980s

While nowadays satellite sea surface temperature images are available several times per day on the internet, the excitement created by the first satellite SST images of the LC south of WA in the early 1980s cannot be overstated. The images showed a number of small offshoots, as had the drifter tracks, with one being linked to an eddy so that it extended over 200 km southward (Legeckis & Cresswell 1981). In addition, and in agreement with the grounded drifters above, images showed that the warm waters of the LC had spread across the shelf to nearshore. Griffiths & Pearce (1985) used satellite imagery to suggest that the offshoots temporarily blocked the flow of the LC and diverted it into unstable baroclinic waves prior to the formation of cyclone-anticyclone eddy pairs. They found the temperature front at the offshore edge of the LC to be as much as 6°C near Cape Leeuwin, but that it was weaker across their images eastward to the Recherche Archipelago.

A sequence of satellite images from 1987 showed that the arrival of the tropical waters of the Leeuwin Current south of WA is a dramatic event: the leading edge of the Leeuwin Current progressed southward to Cape Leeuwin and then eastward at about 20 km day^{-1} between March and April (Cresswell & Peterson 1993). In step with the arrival of the LC there was a decrease in the northward wind stress off the west coast and a decrease in salinity at the Rottnest Island 60 m station at 32°S off Fremantle. At the same time sea level increased at Fremantle and at a pressure recorder on the southern shelf at 116°E. There were some other interesting features in the images: The near shore waters from Cape Leeuwin to 200 km eastward in a March image were cool, probably a result of upwelling from southeasterly winds blowing parallel with the coast and driving the upper waters offshore, to be replaced by a deep onshore flow. The upwelling appeared to feed into what was later named the Capes Current (Gersbach *et al.* 1999). Successive images in April showed a northward intrusion of cold subantarctic water near 118°E to be moving at 0.5 ms^{-1}. The intrusion turned to the east to run alongside the LC. The existence of such intrusions could, in retrospect, be inferred from the tracks and temperatures of the 1970s drifters. Finally, an image in May showed the LC to be interacting with three anticyclonic eddies south of WA.

Thus satellite radiometers and drifters, which respectively monitored the sea surface temperature and the current at the depth of their drogues (20 m), had revealed that the LC reached around Cape Leeuwin and then at least to the Great Australian Bight. The current was strong (up to 1.8 ms^{-1}), it interacted with mesoscale features and subantarctic waters, and part of it spread onto the continental shelf. There was, however, no information on the vertical structure of currents or water properties. For this one would have had to employ research vessels.

Voyages into the LC south of WA in the 1970s and 1980s

In the following paragraphs we discuss the only oceanographic research voyages south of WA in the 1970s and 1980s – by chance all in the same month, June, of each of the years 1971, 1982 and 1987. On each voyage the latest techniques of the time were employed. Hydrocasts at 119°E near Albany in June 1971 by Rochford (1986) from HMAS *Diamantina* showed the LC to flow above the upper continental slope and to have a surface core with temperature exceeding 19.5°C and salinity around 35.7. "Note that salinity is expressed in practical salinity units (International Oceanographic Table, 1981)."

Eleven years later in June 1982 Godfrey *et al.* (1986) ran shipboard and drifter studies of the Leeuwin Current south of WA. The shipboard tools on RV *Sprightly* included a conductivity-temperature-depth profiler (CTD) and XBTs. They mapped a 4°C front at the offshore edge of the LC and found it to be characterized by low Richardson numbers, an indication of considerable interfacial turbulent stresses and overturning. The 15–19°C isotherms at the surface front dipped down to meet the continental shelf edge at about 200 m depth. The front was distorted by an offshoot out to sea that was about 50 km wide and was defined at the surface by the 19°C isotherm, which descended to 90 m on the axis of the offshoot.

In June 1987, the suite of tools to study the Leeuwin Current had expanded to include a hull-mounted Acoustic Doppler Current Profiler (ADCP) on RV *Franklin* and satellite images once or twice per week, within the constraints of cloud cover and the reception range of the Hobart satellite receiving station (Cresswell & Peterson 1993). The LC had a maximum surface speed of over 1.5 ms^{-1} just beyond the shelf edge near 117° E. The trough-shaped near-surface core was 15 km wide between the 0.5 ms^{-1} isotachs and more than 200 m deep. The warm (> 19°C), low salinity (< 35.8) core rode in a U-shaped sheath of higher salinity (> 35.8) subtropical water that had been entrained upstream. Beneath the LC was a reverse flow to the west that probably contributed to the northward flowing LC undercurrent off western WA. A southward offshoot was seen to have strong contrary currents on its western and eastern sides: These ranged up to 0.5 ms^{-1} southward in the west and to 0.5 ms^{-1}northeastward in the east. There was considerable shear in both the horizontal and vertical, with Richardson numbers as low as 0.25. In the course of two days the offshoot pinched off and the remaining anticyclonic bulge on the edge of the LC moved eastward at 0.15 ms^{-1}, faster than similar features observed by Griffiths & Pearce (1985). The current speeds along the curved boundary of the bulge reached 1.5 ms^{-1}. These speeds and the shape of the bulge were similar to those for two anticyclonic meanders travelled by drifters in 1976 (Cresswell & Golding 1980).

These three voyages during the 1970s and 1980s had revealed the vertical structure of the LC, the westward countercurrent that flowed beneath it, and the horizontal and vertical structure of offshoots from it into the open ocean. All three voyages into the study area bounded by Cape Leeuwin and the Recherche Archipelago, the coast and several hundred kilometers southward, were short (less than a week) and the absence of satellite sea surface temperature images for the first two meant that little was known of the larger oceanographic picture. The two images obtained during the period of the third voyage were very useful, but it wasn't until 1994 when data from satellite altimeters, in tandem with daily-updated sea surface temperature images, enabled eddies to be tracked through the study area. Fortuitously, there were three research voyages that year.

Voyages in 1994

As mentioned earlier, 1994 was a special year both because there were three voyages by RV *Franklin* through the study region in July, November and December and because satellite altimeter measurements were available for the first time. Sea surface topography maps (Figures 2A & 2B) derived from measurements by the Topex/ Poseidon and ERS satellites, as well as SST from NOAA satellites, suggested that weak eddies originating east of the Great Australian Bight migrate westward, first encountering the continental slope off the Recherche Archipelago (Cresswell & Griffin 2004). Note that the various eddies shown on Figures 2A and 2B are labelled A, B, C, W, X, and Y. Anticyclonic eddies, labelled A–C on Figure 2, were observed to divert the LC out to sea

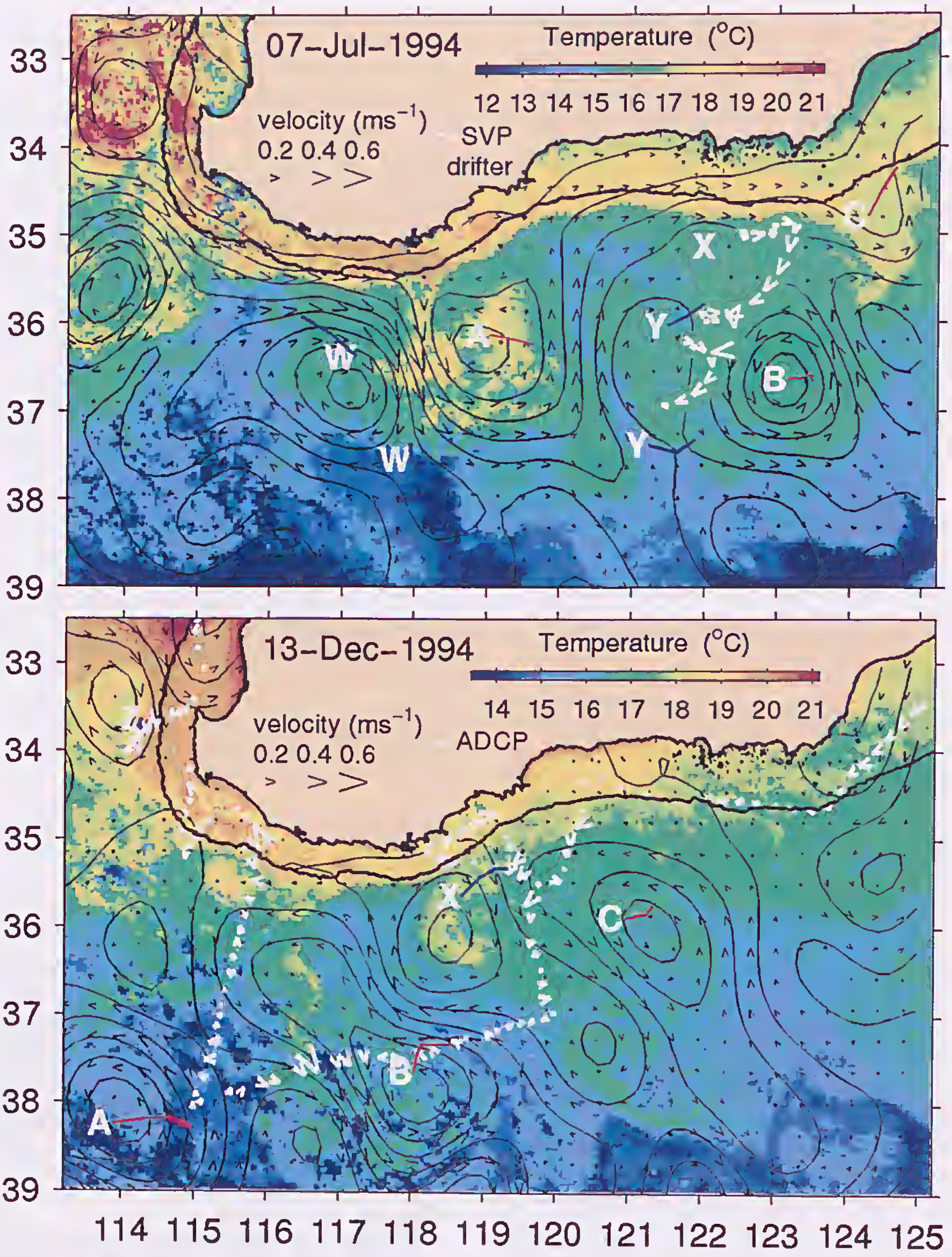

Figure 2a,b. Satellite sea surface altimetry, derived currents and temperature maps for July and December 1994. A, B and C are anticyclonic eddies and W, X and Y are cyclonic. The eddy labeling is automatic and movements of the eddies in the preceding month are marked red /blue for anticyclonic/cyclonic eddies. The white tracks in Figure 2a are the tracks of surface drifters, while in Figure 2b the currents measured by RV *Franklin's* ADCP are marked in white. The shelf edge is marked by a thin black line and a colour scale for the satellite-derived temperatures is shown (Figure kindly provided by David Griffin).

and back again, to capture some of its warm water, and to strengthen as a result. This process was repeated as the eddies drifted westward and occasionally moved near the LC and interacted with it. Cyclonic eddies that moved in against the LC accelerated it eastward along the upper continental slope. Several anticyclonic eddies were followed westward for 18 months as they drifted out into the Indian Ocean at up to 5 km day^{-1}, sometimes splitting, sometimes coalescing. The altimeter data enabled the evolution of oceanographic features to be followed and ship observations to be better understood: For example, we were able to see that the July voyage by chance clipped the NE side of eddy A; the November voyage similarly cut across eddy C; and the December voyage mapped eddy B.

First voyage – July 1994

Franklin voyage FR9407 (Chief Scientist P Petrusevics) from 6–19 July 1994 had been planned to occupy CTD and biology stations along transects from Adelaide to Fremantle. Time ran out near Albany (118°E), but the ship was taken along a zig-zag path to Fremantle and, overall, the voyage yielded an excellent set of current measurements with the vessel's ADCP, which we have processed for this paper. The combined surface topography and temperature image from the time (Figure 2A) shows the LC as a warm stream extending into the Great Australian Bight, along with three anticyclonic

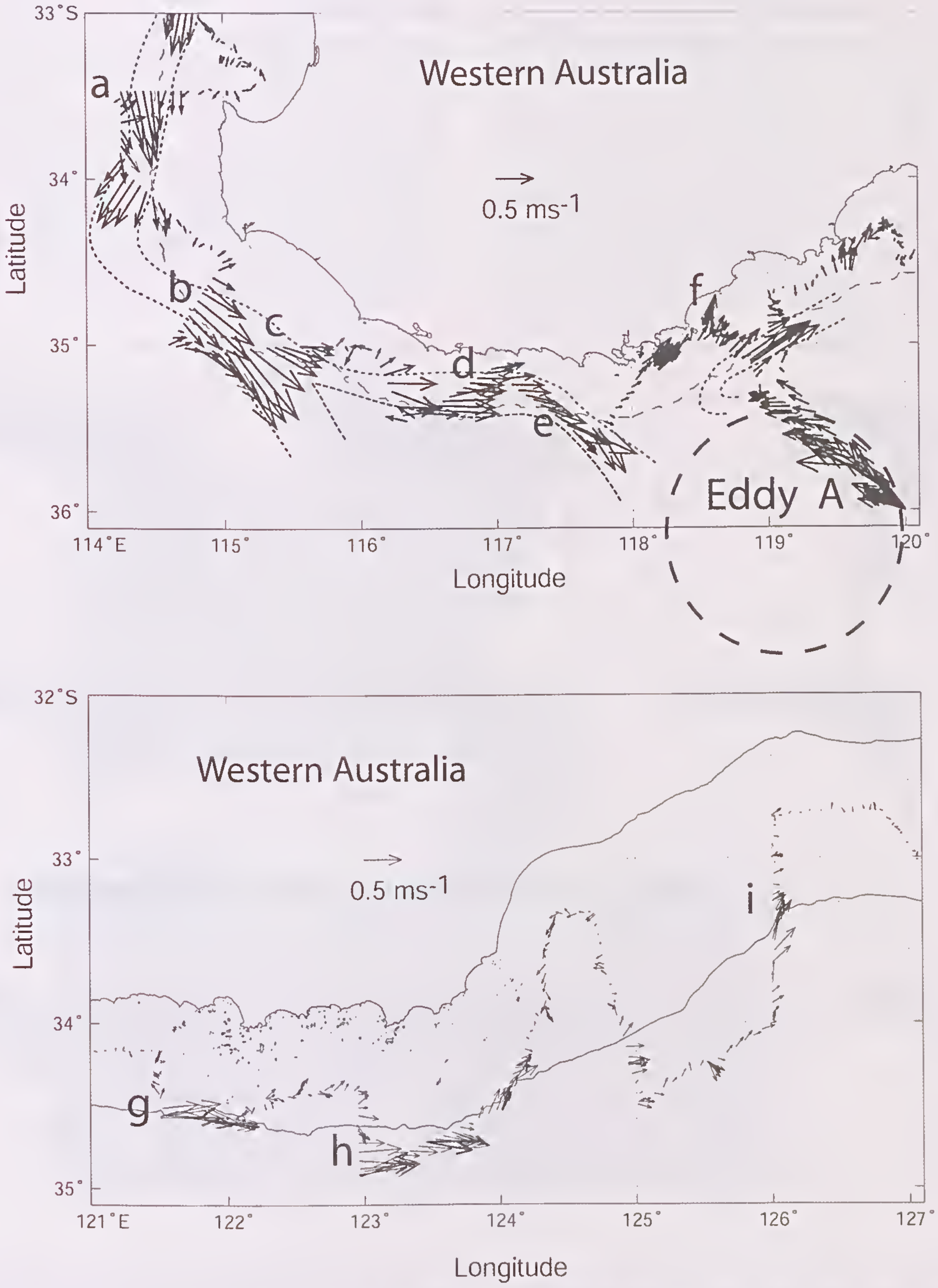

Figure 3. Current vectors at 20 m depth measured by the ADCP on *Franklin* during FR9407, a) from 114 to 120 E and b) from 121 to 127 E. The dotted lines in the former give a conjectured flow path for the LC for speeds greater than 0.5 ms^{-1}. Transects a-i are labeled and the 200 m isobath appears as a thin line.

eddies, labelled A–C, and three cyclonic eddies, labelled W–Y. We note the following features in the image: eddies W and X steepened the sea surface topography from onshore to offshore and thereby accelerated the LC; the edge of the LC bulged seaward across the shelf edge near 115.5°E; the eddy-pair A–W drove a LC offshoot from 118°E out to sea and then around both eddies, more noticeably eddy A; cool subantarctic water flowed northward to the west of eddy W and the east of eddy A; and eddy C was in the process of forming or strengthening in the east of the image. As we will see, voyage FR9407 did not venture sufficiently seaward from the upper continental slope to encounter eddies B and C, but it did cross the NE side of eddy A.

In discussing the ship's ADCP measurements (Figures 3A and 3B, and 4A–4I) we work from west to east – or upstream to downstream with respect to the LC. The LC meandered on and off the outer continental shelf with speeds exceeding 0.7 ms^{-1} from Cape Naturaliste to the Recherche Archipelago. Off the shelf its influence usually reached to 250 m depth, but was sometimes deeper than the depth reached by the ADCP – about 300 m. The LC deviated seaward between Capes Naturaliste and Leeuwin. It was largely on the shelf 100 km farther downstream to the southwest of Cape Leeuwin. It then apparently split, with a major branch heading out to sea – at over 1 ms^{-1} – near 115°E. The other branch moved to be completely on the shelf at 116.5°E, but by 117.7°E this branch deviated offshore. The current speeds on the shelf immediately to the east were very small (0.1 ms^{-1} and smaller), but by 118.5°E the shelf currents had increased to 0.2 ms^{-1} and the LC *per se* ran at 0.8 ms^{-1} right at the shelf edge. It would seem that the seaward offshoot at 117.5°E would have had to have turned back to the shelf for this to be possible – or there was flow from eddy A back into the LC. At 121.5°E the LC was at the shelf edge with a speed in excess of 0.7 ms^{-1}. By 123°E at the Recherche Archipelago the surface core of the LC was 25 km beyond the shelf edge and had a speed again in excess of 0.7 ms^{-1}. At 126°E the LC had a speed of 0.5 ms^{-1} at its core and at longitude of the Head of the Bight, 131°E, 0.3 ms^{-1} (results not shown here). Beyond this it became quite weak and was confused with eddies.

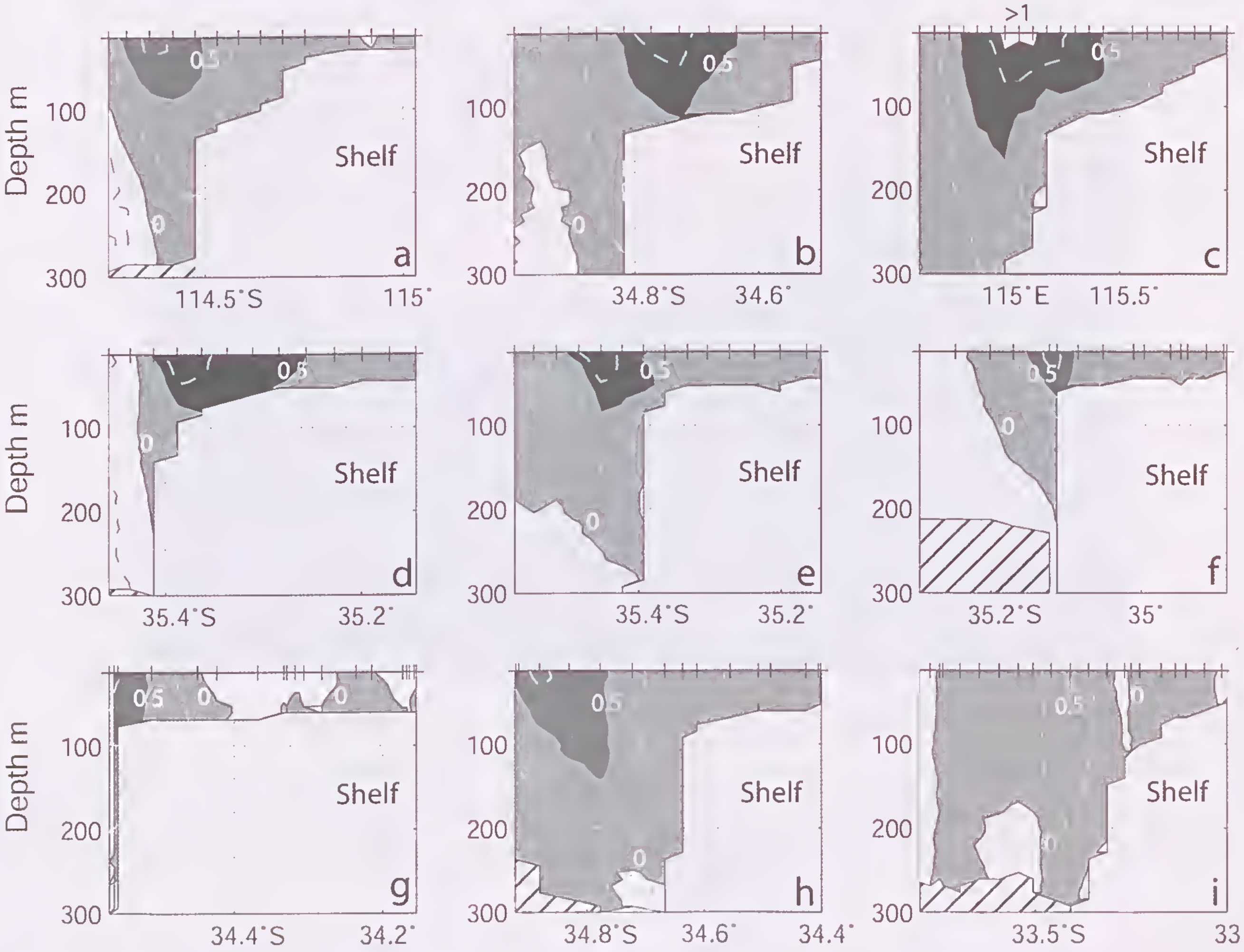

Figure 4. Sections (a-i) showing the downstream (shaded) / upstream (white) current components made with the ADCP on *Franklin* on voyage FR9407 from Cape Naturaliste southward to Cape Leeuwin and then eastward to the western Great Australian Bight. The continental shelf (white) as detected by the instrument is on the right of each panel. The grey shading shows downstream flow of 0-0.5 ms^{-1}; black is for speeds of 0.5-1 ms^{-1} (white near the surface in panel 3 indicates downstream current speeds in excess of 1 ms^{-1}). The contours are separated by 0.25 ms^{-1}. There is noise interference (cross-hatched) near 300 m depth in panels a, d, f, h and i.

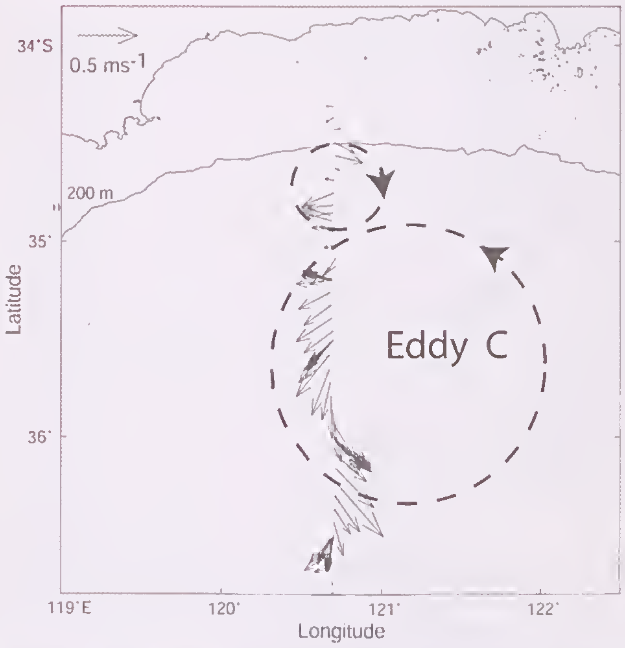

Figure 5. The northern part of a transect made as part of FR9410. The vectors – and satellite sea surface topography from the time – suggest an approximate position of eddy C (dashed line).

Second voyage – November 1994

The second *Franklin* voyage, FR9410, (Chief Scientist M Tomczak) comprised two long transects along 120°E and 132°E to 48 S (Schodlok *et al.* 1997). Here we examine the transect along 120°E, paying attention to the LC and mesoscale features south to 37°S. The transect captured, by chance, the first pass, a chord, across an anticyclonic eddy south of WA. The current speeds in this eddy C reached a maximum of about 0.5 ms^{-1} (Figure 5). The northernmost part of the eddy was at 35.2°S; north of this there appeared to be a small cyclonic cell, with the LC forming its northern side. The LC was weak, with a speed of 0.3 ms^{-1}, but it reached down beyond the outer shelf to more than 300 m (Figure 6A). The current in eddy C decreased very little from the surface to 300 m depth.

CTD stations were occupied only after the ship had moved southward off the shelf (Figure 6B). The surface bowl of eddy C had salinity > 35.5, as did the LC and its cyclonic appendage. Salinity, temperature and other properties are described by Schodlok *et al.* (1997). The SubAntarctic Mode Waters (SAMW) beneath the eddy at 300–700 m depth (salinity and temperature around 34.7 and 9.5°C respectively) can be traced back to the surface at 45°S.

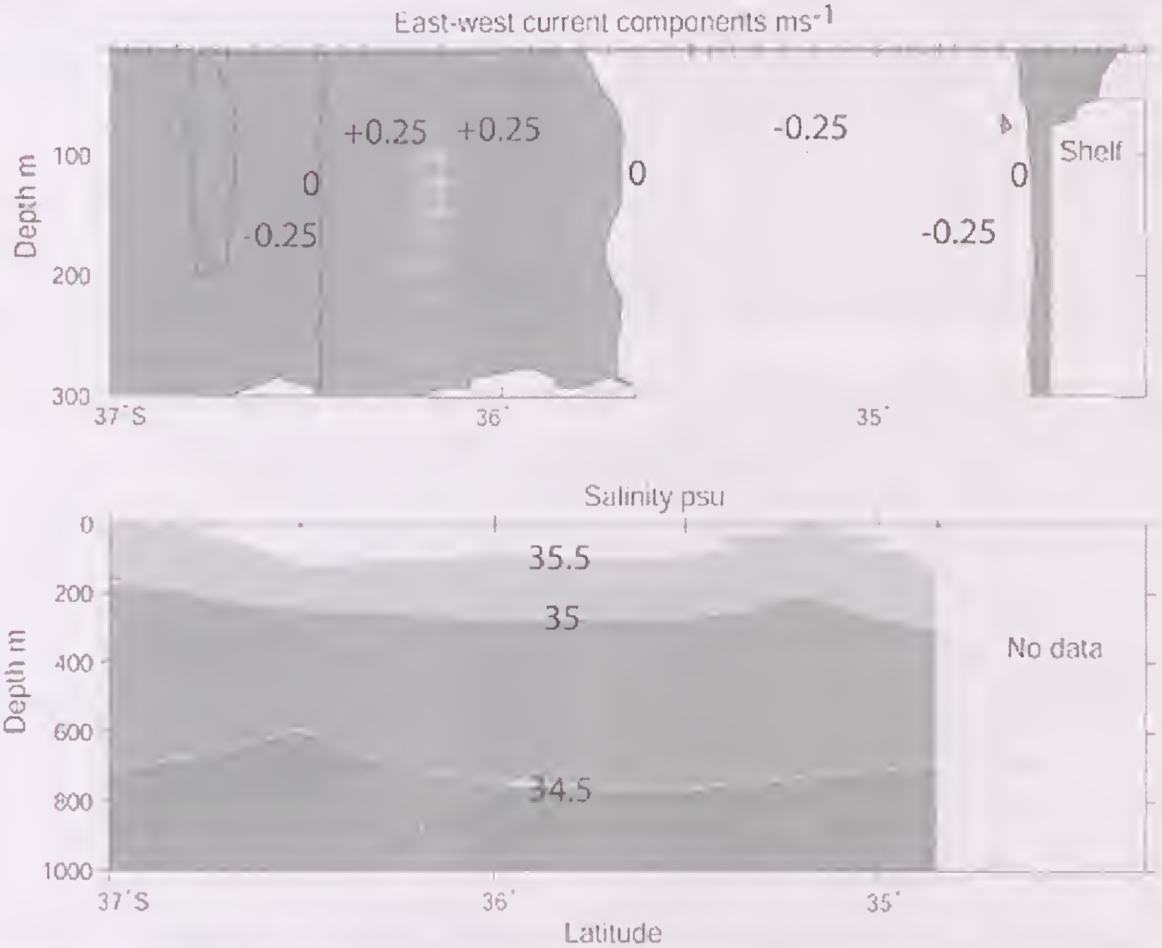

Figure 6. (a) Section made with the ADCP on *Franklin* on voyage FR9407 of the east (grey) and west (white) current component across a chord of eddy C. The continental shelf (white) as detected by the instrument is on the right. The contours are separated by 0.25 ms^{-1}. Thus the eastward component near 36.2°S exceeded 0.25 ms^{-1} as did the westward component near 34.9°S There is noise interference near 300 m depth near 36°S and 36.5°S. (b) The salinity section (to 1000 m) southward from the first station near 34.9°S. The contour spacing is 0.25.

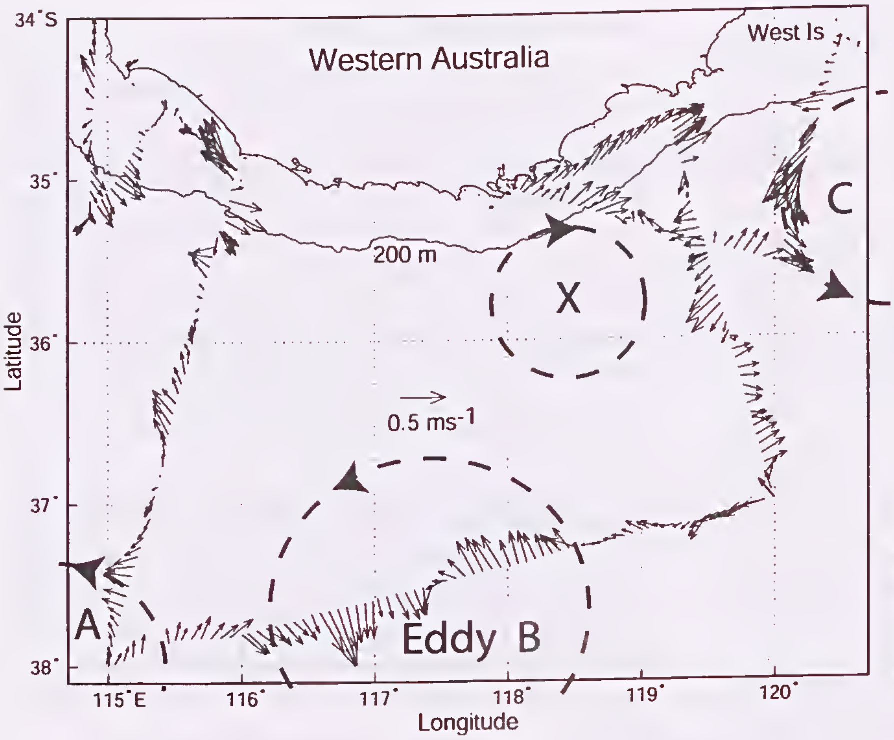

Figure 7. Current vectors at 20 m depth measured by the ADCP on *Franklin* voyage during FR9411. The positions of anticyclonic eddies A-C and cyclonic eddy X, as estimated from both the satellite topography and the vectors measured by the ship, are marked.

Third voyage – December 1994

The third *Franklin* voyage, FR9411 (Chief Scientist G Cresswell), went from Pt Lincoln to Fremantle. A number of findings were presented by Cresswell & Griffin (2004) and we will summarise those, as well as examining the data in a manner that complements the two earlier 1994 voyages. The surface topography and temperature image from the time Fig.2B shows anticyclonic eddies A–C as well as cyclonic eddy X near the shelf edge at 118.5°E; eddy X was in a position to strengthen the LC, whereas eddy C would have weakened it. Cold subantarctic water was driven northwestward on the eastern sides of eddies A and B.

The ship occupied CTD stations along the route and took current and other underway measurements. It crossed Eddy B with the aid of a satellite thermal image and this is obvious in the map of current vectors (Figure 7). The effects of eddies C and X on the current patterns are complex and difficult to interpret. The LC was detected near the shelf edge at 115°, 116° and around 119°E, where cyclonic eddy X may have strengthened the currents and spread them onto the shelf. Just to the east of 120°E the vectors may show the influence of eddy C. On the shelf in the west there was flow, perhaps wind-driven, towards and beyond Cape Leeuwin that contributed to the Capes Current.

Eddy B had a bowl-shaped cross section (Cresswell & Griffin 2004) in temperature and salinity and perturbed the structure down to at least 1000 m. The currents decreased very little from the surface to 300 m. Nutrients and oxygen were low in the centre of the eddy; there was a fluorescence maximum at 80–100 m and this extended up to the surface around the perimeter of the eddy at 116°E and 119.5°E.

Figure 8 shows salinity and temperature profiles and the T–S diagrams from a station nearest the centre of eddy C in November; from one nearest the centre of eddy

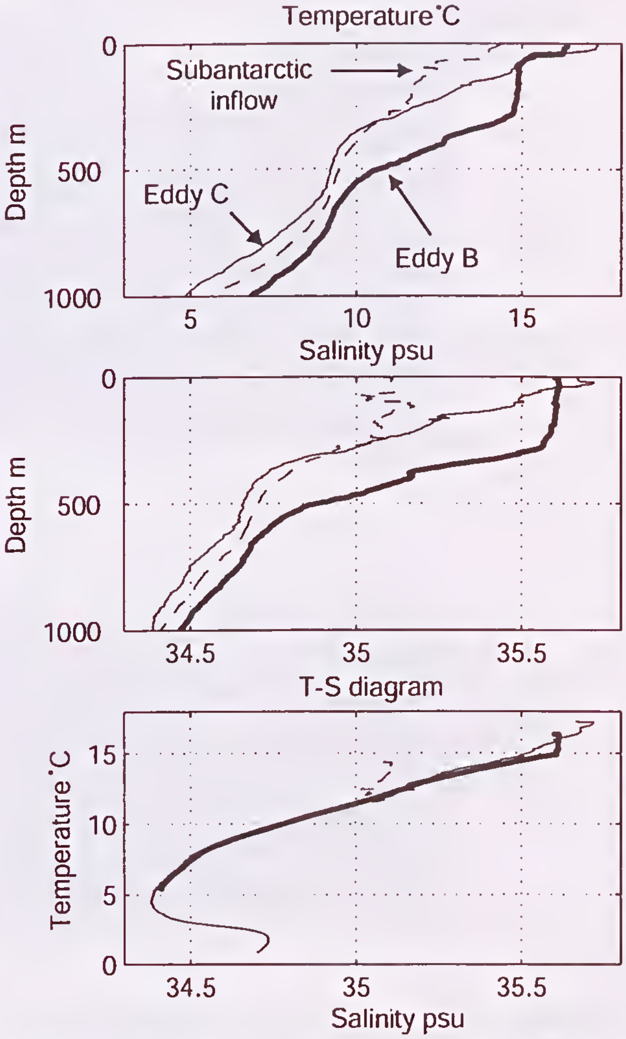

Figure 8. Salinity, temperature and T-S profiles from stations in eddy C in November, eddy B in December, and the subantarctic waters flowing northwestward between eddies A and B in December 1994.

B on December; and from one in the northwestward-flowing subantarctic water between eddies A and B in December. Eddy C showed no evidence for a deep winter mixed layer, probably because it formed off the Recherche Archipelago late in winter (August). Eddy B had a deep winter mixed layer to 290 m with a warm "summer cap" from insolation. Note that salinity was constant through this layer. The subantarctic upper waters can be seen to be relatively cool and fresh. The December stations were only taken to a little over 1000 m and they did not quite reach the salinity minimum of the Antarctic Intermediate Waters, but this can be seen in the T–S profile of the November station that was taken to the bottom. The SubAntarctic Mode Waters formed by deep winter mixing near 45°S are marked by the steeper slopes near 9°C and 34.65 in the temperature and salinity profiles. The temperature and salinity profiles emphasize the 300 m depression of the water structure caused by eddy B.

The observations for 1994 discussed above represent the first example of combining satellite sea surface topography and temperature measurements with research vessel measurements in Australian waters. The observations enabled eddies to be monitored for up to two years and examined in detail as they drifted westward into the region south of WA. They evolved and interacted with the LC and with one another before finally drifting westward into the Indian Ocean. The July 1994 voyage gave the first synoptic picture of the LC as it meandered on and off the shelf between Cape Naturaliste and the Recherche Archipelago. There remained a gap in knowledge about the temporal variability of the currents on the continental shelf, which leads us to the next section.

A mooring at 80 m near the Recherche Archipelago in 2001/02

Until 2001 no current meters had been moored on the shelf or slope south of WA and therefore little was known of the variability of the currents with time. To address this a mooring deployed at 34.125°S, 121.58°E at the 80 m isobath at the mouth of Causeway Channel some 22 nautical miles southwest of Esperance and 15 nautical miles west of the plateau on which stand many of the islands of the Recherche Archipelago (Figure 9).

Aanderaa current meters at 30 and 60 m depth collected data on speed, direction and temperature from November 2001 to August 2002 and here we present for the first time some of the results. The temperature time series (Figure 10A) show that the waters were mainly stratified over summer until mid-March, when they became mixed due to the arrival of the Leeuwin Current and/or the effects of winter heat loss and overturn. The current measurements (Figure 10 b) suggest that the rotor on the lower meter either stuck or fell off after two months. The monthly progressive vector diagrams (Figure 11) showed the current flow to be predominantly in the direction of the Great Australian Bight, apart from November and February, being strongest in May, June,

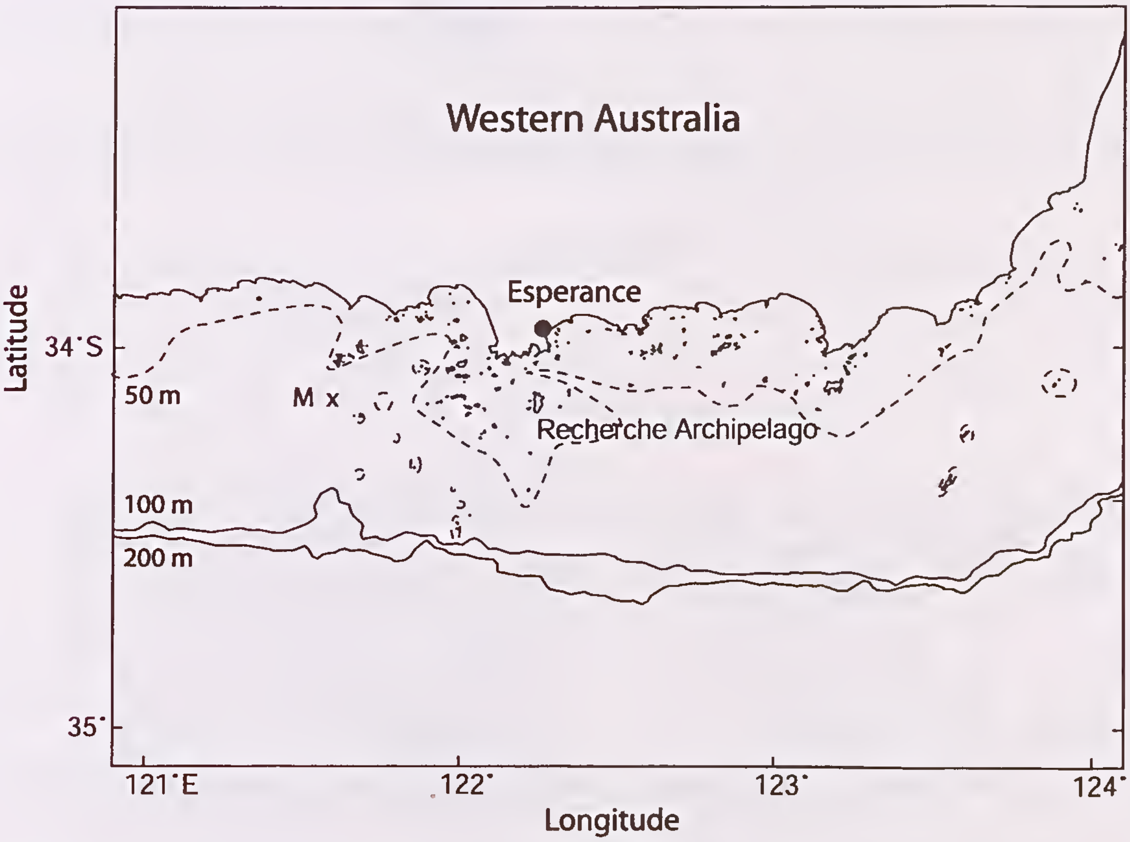

Figure 9. A chart of the location of the mooring (M) showing the coastline and the 50, 100, and 200 m isobaths. The islands form the Recherche Archipelago and the city of Esperance is marked.

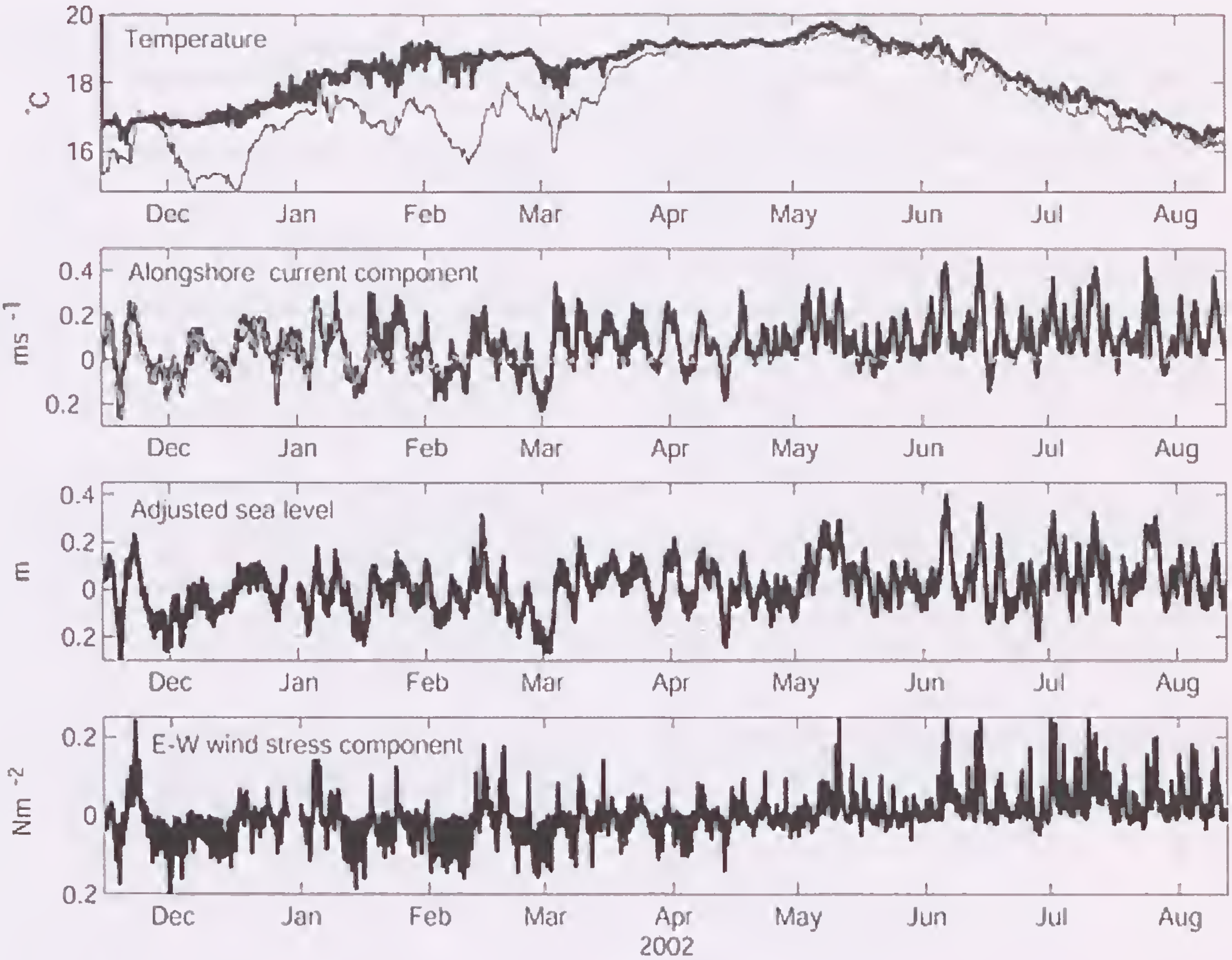

Figure 10. Time series of a) temperature for the upper (thick line) and lower (thin line) current meters; b) alongshore current for the upper meter onto which is superimposed the alongshore current for the lower meter until it failed in early February; c) adjusted sea level at Esperance; and d) the east-west wind stress at Esperance.

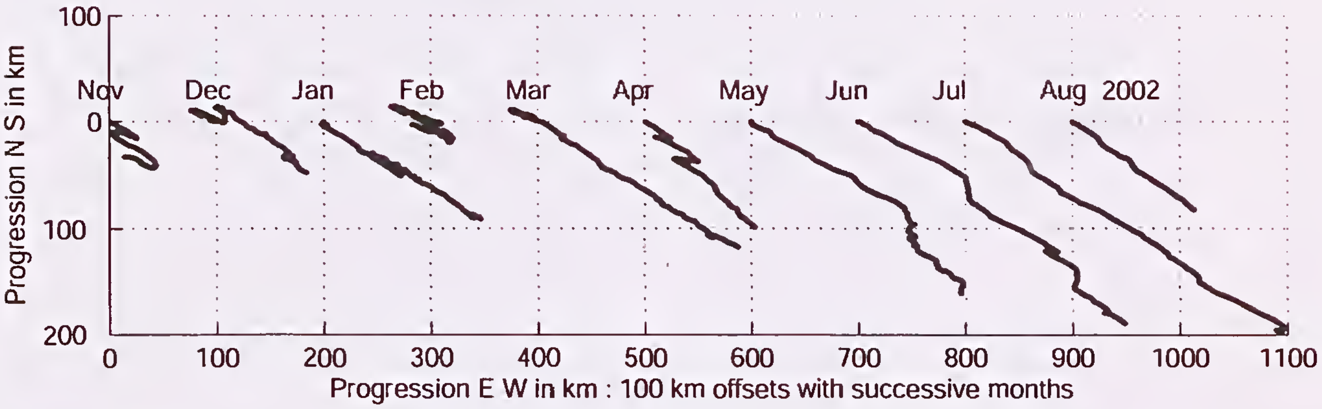

Figure 11. Monthly progressive vector diagrams for the upper meter (30 m depth); November 2001 and August 2002 are not complete months.

July (> 0.1 ms^{-1}, or more than 10 km day^{-1}) and August, and to be diverted to the SSE apparently by the presence of the raised topography of the Recherche Archipelago immediately downstream. Figure 10B shows the flow in the SSE direction and it is referred to as the "Alongshore current component". The strong winter (May/August) flow towards the Great Australian Bight was accompanied by higher sea level (Figure 10C) and stronger eastward wind stress (Figure 10D). The sea level measurements from Esperance were adjusted for the inverse barometer effect (relative to a rough annual average sea level pressure of 1017 hPa).

While there was some agreement between the alongshore current and the eastward wind stress at intervals of several days, there was much better agreement between the current and the adjusted sea level. This was probably due to both parameters responding to passing coastal-trapped waves (Provis & Radok 1979; Church & Freeland 1987) that were generated by weather forcing further west or nearby.

We examine two wind-related events: the oscillating current in November (summer) and a large current pulse in the first week in June. For the former, Figure 12 shows 12 days of the alongshore current components for the two instruments, the adjusted sea level at Esperance, and the east west wind stress component, together with atmospheric pressure maps at times of the extremes of the current oscillations. The current trough, or flow of

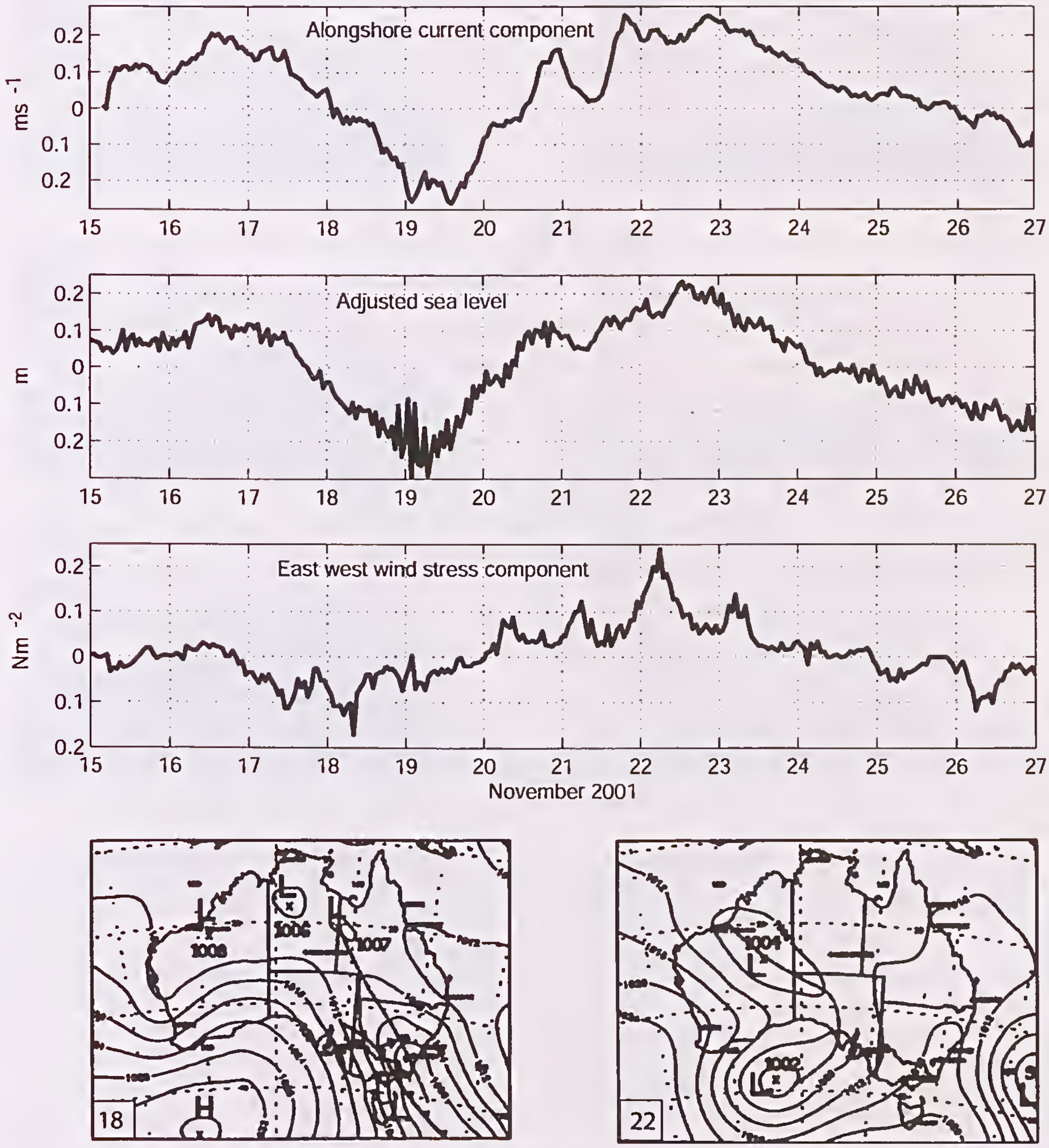

Figure 12. An oscillation in the alongshore current related to the passage of atmospheric pressure features and associated wind forcing: a) alongshore current component 15-27 November 2001; b) adjusted sea level; and c) east-west wind stress. Bottom panels: sea level pressure maps for 18 and 22 November 2001.

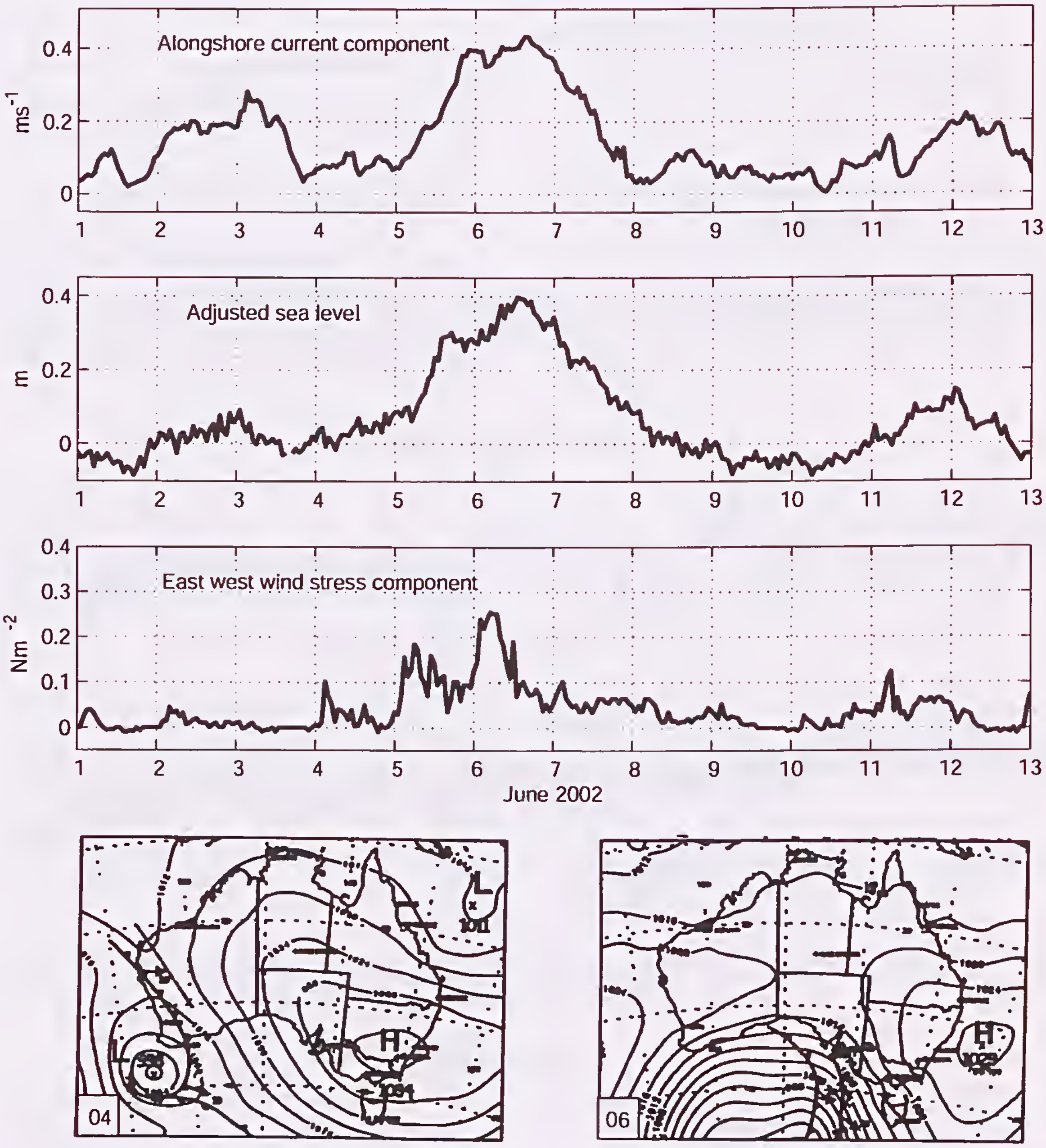

Figure 13. An alongshore current pulse related to the passing of atmospheric low pressure features and associated wind forcing: a) alongshore current component 1-13 June 2002; b) adjusted sea level; and c) east west wind stress. Bottom panels: sea level pressure maps for 4 and 6 June 2002. a) current component time series 3-10 June 2002; b) sea level pressure map for 4 June 2002; c) sea level pressure map for 6 June 2002.

0.25 ms^{-1} towards Cape Leeuwin, followed enhanced westward wind stress from a high pressure cell centred south of the Great Australian Bight. The subsequent current crest, or flow towards the Archipelago, was due to eastward wind stress from a low in the Bight. The current variations were closely related to sea level variations. The wind stress parallel with the coast would have raised/lowered sea level due to the Ekman effect depending on whether it was eastward/westward. The sea level slope across the shelf would have driven the the alongshore currents.

There was a strong (0.4 ms^{-1}) pulse in the alongshore flow towards the Great Australian Bight on 6/7 June 2002 (Figure 13). It was closely related to a crest in the sea level and it followed enhanced eastward wind stress that was due to a deep low pressure cell travelling eastward to south of the continent. The interval, 1–13 June, shown in Figure 13 included two other current pulses on 2/3 June and 12 June. These were related to sea level crests, but the wind stress at the time was not great. Perhaps these current pulses were the result of coastal-trapped waves propagating into the region from the west.

To conclude this section we have seen that the LC usually extends onto the continental shelf and that it is steered seaward by the topography of the Archipelago immediately to the east. Also, passing weather systems and coastal-trapped waves have strong effects on the circulation.

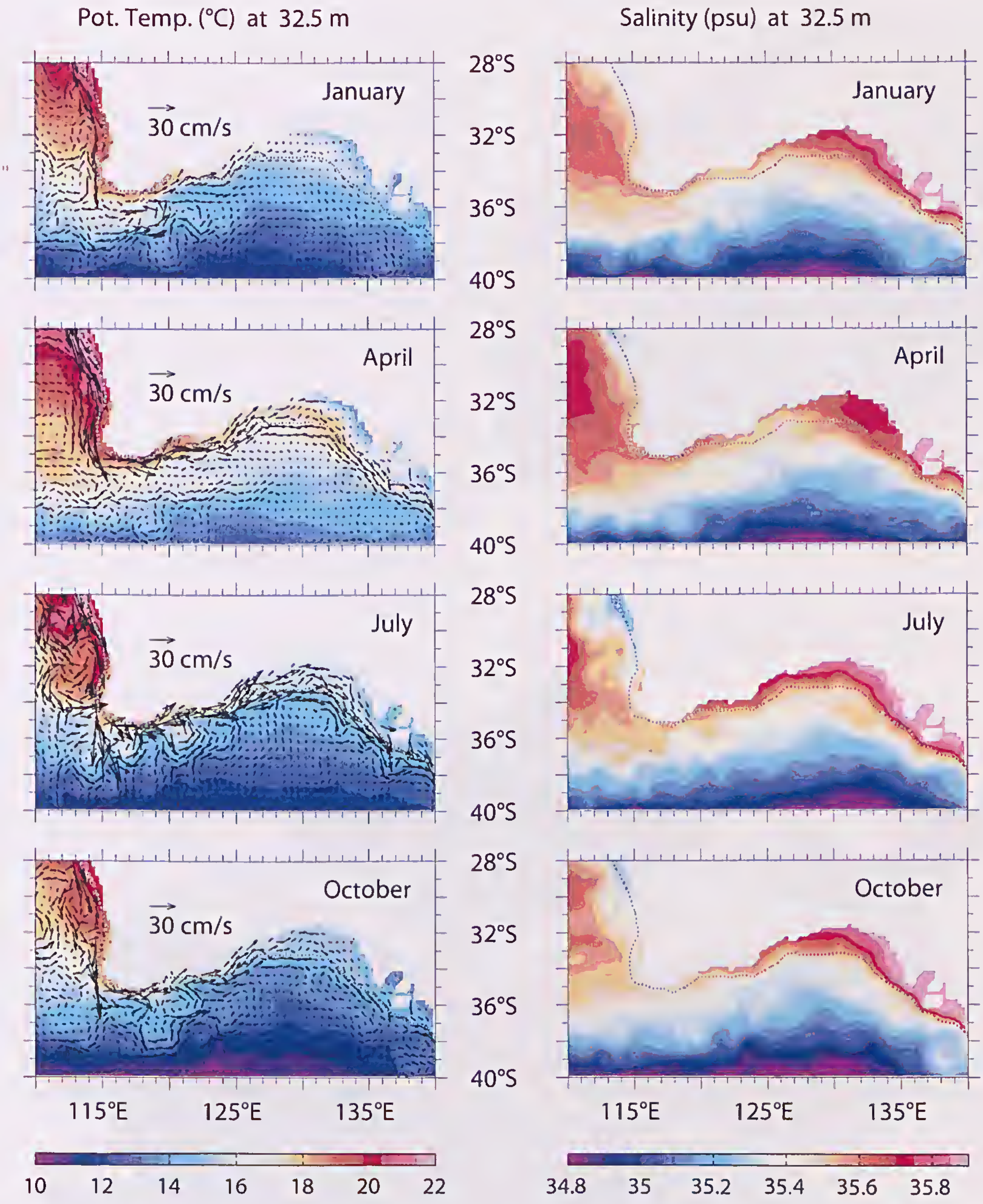

Figure 14. Seasonal variability of the Leeuwin Current in the 0.28° Los Alamos National Laboratory Parallel Ocean Program (POP) ocean model. Potential temperature (lef panels), salinity (right panels) and velocity vectors at 32.5 m (core depth). Velocity vectors were plotted at every other point for clarity.

Model results

We examine the seasonal variability of the Leeuwin Current, along the southern part of the west Australian coast and along the eastern part of the south Australian coast, using 5-year monthly mean simulated fields of near-surface temperature, salinity and velocity from the 0.28° Los Alamos National Laboratory Parallel Ocean Program (POP) ocean model (Maltrud *et al.* 1998; Garfield *et al.* 2001). Qualitatively, this model was shown to reproduce the major components of the observed mean state, low-frequency variability and hydrographic properties of the near-surface circulation associated with the Leeuwin Current and its undercurrent along the

Western Australia coast (Domingues 2006), from North West Cape (22°S) to Cape Leeuwin (34°S).

In agreement with *in situ* observations (*e.g.*, this study) and remotely-sensed observations (*e.g.*, Legeckis & Cresswell 1982; Ridgway & Condie 2004), the simulated fields in Figure 14 illustrate the seasonal progression of the Leeuwin Current into the Great Australian Bight. From December to March, the boundary flow of the Leeuwin Current is quiescent. It suddenly pulses in April and evolves into a vigorous current during austral winter. The eastward flow of the Leeuwin Current in the Great Australian Bight is initially strongest only on the western part of the basin but by July/August it has accelerated along the entire basin. The vigorous flow then becomes unstable and dissipates a large amount of its energy by shedding mesoscale eddies. This energetic winter time eddy variability, along the outer edge of the Leeuwin Current, is clearly manifested in the July panel, even though it represents a 5-year average (1993–1997). From September to November, energy levels gradually decay and the quiescent summertime phase of the Leeuwin Current is restored.

The generation of mesoscale eddies by the vigorous flow of the Leeuwin Current is not only a form of dissipating energy (Feng *et al.* 2005) but also a way of exchanging water properties and other tracers. Domingues *et al.* (2006) found that 70% of the heat advected into the coastal region off Western Australia, by the narrow poleward flow of the Leeuwin Current, is transferred to the adjacent ocean interior through eddy fluxes. This is the primary means by which the Leeuwin Current is cooled along its boundary path (about 5°C over 1350 km). A Lagrangian particle tracking performed during the POP model run (Domingues *et al.* 2007) additionally showed that particles seeded within the Leeuwin Current off Western Australia can be advected as far as the west coast of Tasmania within a 5-year (or less) timescale, and many others can become trapped for prolonged periods in the energetic mesoscale eddies, mostly around Cape Leeuwin. Trapped particles were either seen to gradually subduct and return to Western Australia as part of the equator-ward flow of the Leeuwin Undercurrent or drift westward within the eddies. The latter appeared to be the most common situation.

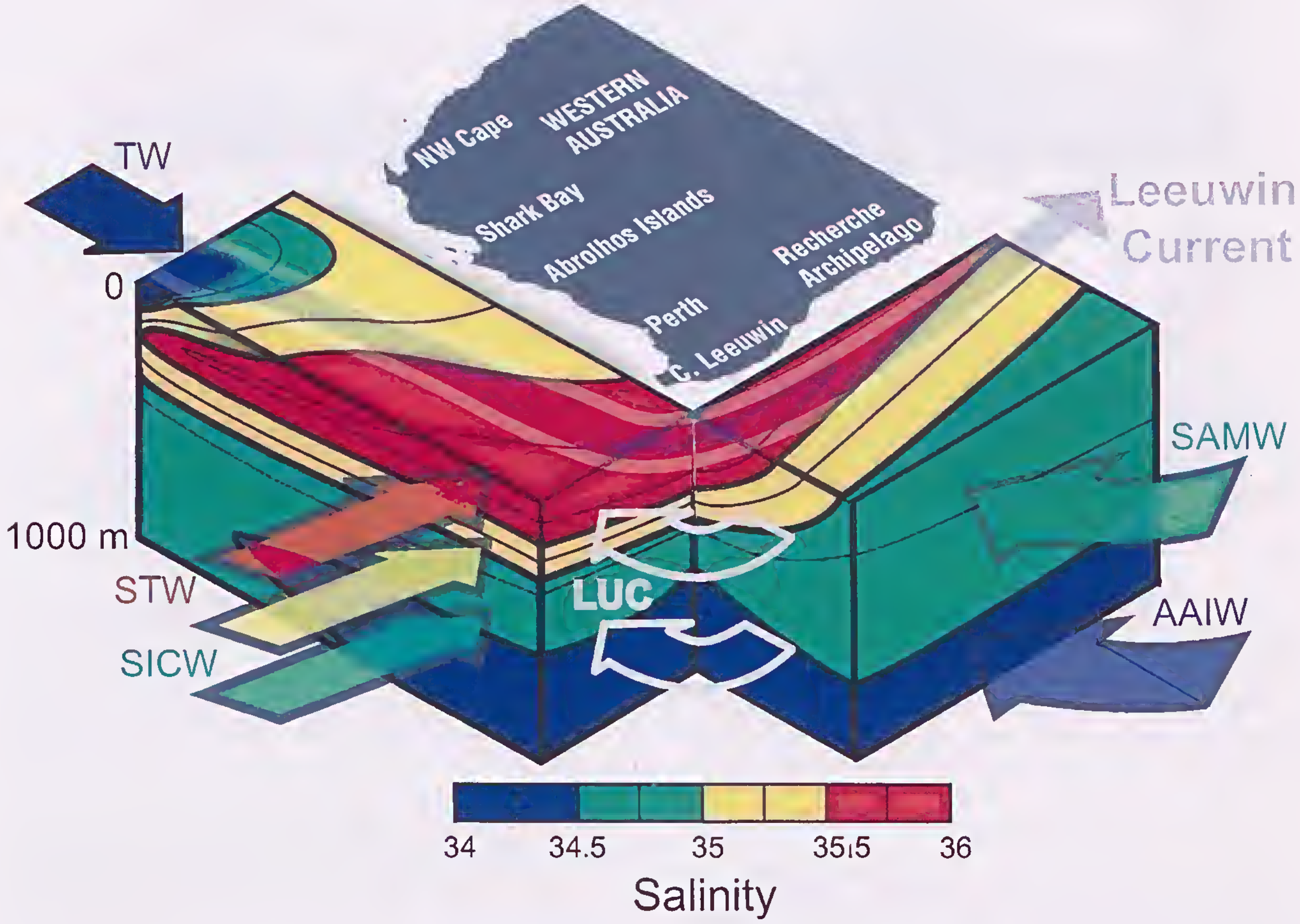

Figure 15. A schematic diagram of the salinity structure down to 1000 m drawn from several ship surveys. The boxes are 1000 m deep and about 200 km wide. The view is from above the southern Indian Ocean and the map is to orient the reader.

Discussion

The interplay of the various water types to the west of WA has been summarized in a schematic diagram by Woo (2005). This inspired Figure 15, which should simplify this discussion. It was drawn from salinity data collected on several voyages by RV *Franklin* in 1987 and 1994; it excludes shelf waters and eddies. The main inputs to the near-surface Leeuwin Current system are the low salinity tropical waters in the north (blue, TW); the salty sub-tropical waters in the west (red, STW); and, to a lesser degree, the relatively fresh subantarctic waters in the south (green). The salty subtropical waters split, with one part moving northward and deepening, while the other moves southward and then eastward around Cape Leeuwin thereby making the Leeuwin Current a relatively salty stream south of WA.

Flowing westward along the southern continental slope to Cape Leeuwin and then northward is the Leeuwin Undercurrent, which Ridgway (2007) has shown to be part of a "supergyre" traversing both the Pacific and Indian Oceans. The other inputs to the depth range from several hundred to one thousand metres are the South Indian Central Water in the west (yellow and green arrows, SICW) and the SubAntarctic Mode Water (green arrow, SAMW) and Antarctic Intermediate Water (blue arrow, AAIW) in the south. Not shown in the east is the Flinders Current (Middleton & Bye 2007) which feeds into the Leeuwin Undercurrent south of WA.

The schematic diagram is expanded for the region south of WA (Figure 16) to show surface currents due to the Leeuwin Current and eddies – one anticyclonic and two cyclonic. As we have seen, there can be several anticyclonic eddies between the longitudes of Cape Leeuwin and the Recherche Archipelago. The diagrams draw on observations taken by Cresswell & Peterson (1993) and Cresswell & Griffin (2004). Sometimes the eddies are too far offshore to influence or interact with the Leeuwin Current, or at other times a bulge may form on the seaward side of the LC adjacent to an anticyclonic eddy. The bulge can develop into an offshoot that will carry LC water out to sea and around the eddy, which then takes on some of the warm salty waters and strengthens. Part of the offshore flow often encircles the adjacent cyclonic eddies, as was revealed by drifters.

The LC attains maximum speeds of 1.8 ms^{-1} between rounding Cape Leeuwin and reaching the Recherche Archipelago as it moves on and off the continental shelf. The offshoots of the LC can have complex structure, with south-going currents of up to 0.5 ms^{-1} on their western sides and north-going ones of similar speeds on the eastern sides. Strong current shear leads to turbulence and overturning. Some of the eddies may propagate into the region from across the Great Australian Bight and then strengthen as a result of interacting with the LC to the south of the Recherche Archipelago. The eddies can be followed with satellite altimetry at least for two years as they drift westward south of WA and then out into the Indian Ocean.

A summer survey of an anticyclonic eddy showed influences of the LC, deep mixing in winter, and summer heating that formed a cap to the temperature structure. This was similar to structures seen in the East Australian Current anticyclonic eddies described by Nilsson & Cresswell (1980). The subantarctic water around the eddy was cooler, fresher, and richer in nutrients and oxygen than both the eddy and the LC. Two of the eddies that were crossed south of WA had maximum surface current speeds of about 0.5 ms^{-1}; these speeds decreased only slightly down to the 250–300 m reached by the Acoustic Doppler Current Profiler.

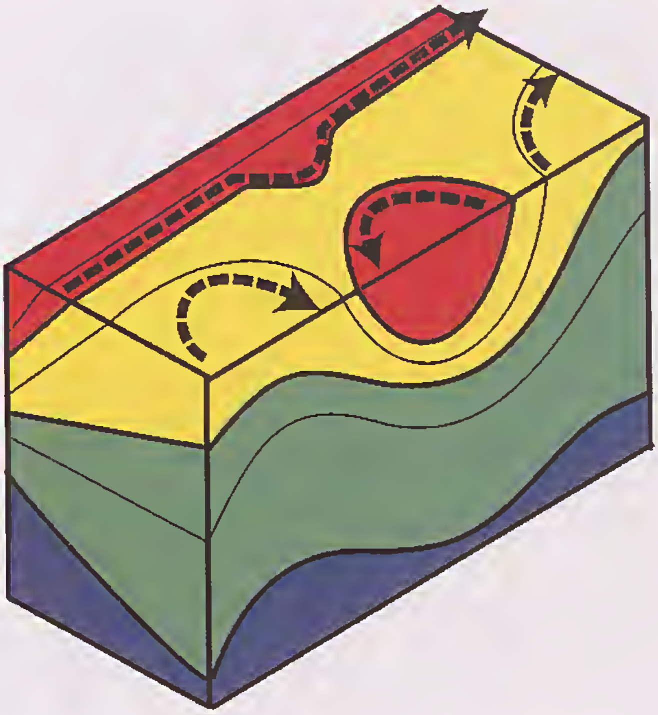

Figure 16. A schematic diagram of the salinity structure down to 1000 m as for Figure 15, but only for the region south of WA, and showing the Leeuwin Current and mesoscale features. The colour scale is as for Fig. 15.

The waters of the Leeuwin Current spread across the southern continental shelf and into the coast. This was suggested by the grounding of two drifters in the 1970s and by satellite images that showed warm waters extending across the shelf with only slight cooling very close to the coast. Midway across the shelf, at a mooring at the 80 m isobath 25 km to the west of the Recherche Archipelago, the LC was the main circulation feature. It was turned seaward there by the downstream proximity of the Archipelago. The other main influence came from the winds from passing weather systems which variously reversed and accelerated the current.

As was mentioned earlier, Wood (1954) suggested that there was an ocean current that flowed from Western Australia to Tasmania. Other support for the idea that the Leeuwin Current could act as a conduit to bring tropical and subtropical marine fauna and flora to southern Australia can be found in Colborn (1975), Krey & Babenerd (1976), Maxwell & Cresswell (1981), Hallegraeff (1984), Wells (1985), and Gaughan & Fletcher (1997). We conclude this discussion with a chronology of the evolution of our understanding of the LC south of WA (Table 1).

Table 1

A chronology of key observational findings in the study area south of WA between Cape Leeuwin and the western Great Australian Bight

Period	Type of study	Key findings
Early 1800s	Navigation with sextant and logline	A 0.6 ms^{-1} current to the east where we would now expect the LC
Early 1900s	As above, plus "Challenger" expedition observations	The flow of warm water southward to Cape Leeuwin and then eastward
1950s	Phytoplankton distribution	An inferred current from Cape Leeuwin to Tasmania
1960s	Hydrocasts	Inflow at 30 S of salty Indian Ocean water towards WA
1970s	Expendable bathythermographs	The southward turning of this inflow through a field of mesoscale eddies to Cape Leeuwin
1970s	Satellite tracked drifters	An energetic southward flow to Cape Leeuwin and then eastward at speeds up to 1.8 ms^{-1}. Interactions with mesoscale eddies and offshoots out to sea. The Leeuwin Current named.
1971	Hydrocasts	Temperature and salinity section shows Leeuwin Current flowing near the upper continental slope near Albany
1980s	Satellite sea surface temperature images	Synoptic images of Leeuwin Current fronts, eddies and offshoots and the spread of the current to the nearshore. Plumes of subantarctic water seen to move northward to interact with the Leeuwin Current. One image showed upwelling near Cape Leeuwin. Other images captured the eastward progression of the Leeuwin Current "nose" at 20 km day^{-1} in autumn.
1982	Expendable bathythermographs, water property profiler (CTD) and drifters	Sections across the Leeuwin Current, a cyclonic eddy and a current offshoot.
1987	Research vessel observations with water property (CTD) and current (ADCP) profilers	Sections across the Leeuwin Current and an offshoot from it. The flow south of WA included both tropical and subtropical waters Speeds exceeded 1.5 ms^{-1} in the Leeuwin Current and there were contrary flows within the offshoot. Beneath the Leeuwin Current there was westward flow at 400–700 m.
1994	Three voyages with CTD and ADCP plus satellite topography images and inferred currents, as well as satellite temperature images	Anticyclonic eddies were followed for as they drifted westward through the study area and beyond into the Indian Ocean. Both anticyclonic and cyclonic eddies interacted with the Leeuwin Current. The properties of the various features were mapped.
2001–02	Current meter mooring at the 80 m isobaths near the Recherche Archipelago	A significant Leeuwin Current influence for all months except November and February, with the winter months being strongest and May having a mean current of 0.13 ms^{-1}. The winds from intense passing weather systems variously reversed and accelerated the current. Coastal-trapped waves also had similar strong effects.

Conclusions and suggestions

Evolving observational techniques over the past two centuries have led to the following conclusions:

The Leeuwin Current south of WA:

- Brings low salinity tropical and high salinity subtropical waters to Cape Leeuwin and thence eastward into the low salinity subantarctic regime south of WA.
- Is present most of the year, but is strongest in autumn/winter following the eastward progression of its leading edge at about 20 km day^{-1} between March and April.
- Meanders on and off the continental shelf from Cape Naturaliste to the Recherche Archipelago with speeds off the continental shelf as high as 1.8 ms^{-1} and a depth penetration to 250m.
- Is weaker (0.3–0.5 ms^{-1}) to the east of the Recherche Archipelago and into the Great Australian Bight
- Is diverted out to sea around anticyclonic eddies that take on some of its waters
- Is accelerated eastward on the northern sides of cyclonic eddies
- Was detected most of the time from December 2001 to August 2002 at a current meter mooring at the 80 m isobath on the continental shelf near the Recherche Archipelago. The shelf currents were also strongly influenced by winds from passing weather patterns and by passing coastal-trapped waves.

The anticyclonic eddies:

- Drift westward across the Great Australian Bight to interact with the Leeuwin Current and strengthen near the Recherche Archipelago
- Interact with the Leeuwin Current, subantarctic waters, and one another as they drift westward to the longitude of Cape Leeuwin and then out into the Indian Ocean.

- Influence the water structure down to at least 1000 m depth
- Have current speeds that decrease very little from the surface down to 250–300 m depth.
- Develop deep mixed layers (to 300 m) if they spent several winter months in the study area
- Are low in nutrients and oxygen.

The tasks that we know to remain include achieving a better understanding of:

- The effects of winds and the LC on the waters across the entire continental shelf south of WA, rather than just at the 80 m isobath near Esperance
- Does upwelling occur to the same degree at the Recherche Archipelago as it does immediately to the east of Cape Leeuwin?
- The effects of the differing bottom topography along the shelf and upper slope – the precipitous shelf edge cliffs, the changing shelf width, the barrier presented by the Recherche Archipelago.
- The responses of living organisms to the dynamic oceanographic features.
- Why the 1970s drifters interchanged with the Leeuwin Current and cyclonic eddies and not with anticyclonic eddies.

These will require observations with research vessels, numerous long-term moorings, gliders, and satellite remote sensing, to name a few.

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Larval fishes off Western Australia: influence of the Leeuwin Current

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Abstract

Although the poleward flow of the Leeuwin Current off Western Australia is unique among eastern boundary currents in the southern hemisphere, the biological oceanography of this system is comparatively poorly known. In this short review, the findings of the various studies on larval fishes completed off Western Australia are collated, synthesized and related to the influence of the Leeuwin Current. The studies range from light-trap experiments focusing on tropical fish larvae off the north-western coast to studies on larvae of commercially significant temperate clupeiod species in the Great Australian Bight. Larval fish assemblages within the Leeuwin Current appear to be composed of a mixture of oceanic, slope, tropical and temperate coastal species, with strong seasonal variation in species composition. Ichthyoplankton studies in progress off Western Australia are reported on and aim to address gaps in the knowledge about the influence of the Leeuwin Current and its meso-scale features upon larval fishes.

Keywords: Leeuwin Current, ichthyoplankton, sardines, water masses, eddies

Introduction

The Leeuwin Current is an atypical eastern boundary current in the Indian Ocean that flows poleward along the shelf-edge off Western Australia (WA) before turning eastward at Cape Leeuwin and crossing the Great Australian Bight (Cresswell & Golding 1980). This warm, low salinity current is driven by a strong alongshore steric height gradient that is sufficient to suppress the effects of coastal wind-driven upwelling (Ridgway & Condie 2004). This results in oligotrophic conditions, unlike the highly productive eastern boundary currents off South America and southern Africa (Pearce 1991; Feng *et al.* 2009).

Studies of larval fish assemblages have been conducted in most of the world's major boundary currents, for example, the California Current, Gulf Stream, Benguela Current and Agulhas Current (Doyle *et al.* 1993; Moser & Smith 1993; Olivar & Shelton 1993; Beckley 1998; Hare *et al.* 2001). Western boundary currents such as the Gulf Stream, Agulhas Current and East Australian Current provide a transport mechanism for larvae of tropical fishes to be dispersed towards temperate areas (Miskiewicz 1989; Gray 1993; Olivar & Beckley 1994; Beckley & Leis 2000; Hare *et al.* 2002; Booth *et al.* 2007). Although southward dispersal of larval fishes by the Leeuwin Current has been invoked in the literature (Maxwell & Cresswell 1981; Hutchins 1991; Lenanton *et al.* 1991; Hutchins & Pearce 1994; Caputi *et al.* 1996), there has been no specific study of the ichthyoplankton of the Leeuwin Current *per se*. However, there have been several localized studies which have investigated larval fishes in specific areas along the WA coast. In this short review, we will draw these together, synthesise their findings and relate them to the Leeuwin Current. The review will sequentially cover the three broad geographical areas off WA, namely the north-west, west and south coasts as well as the implications of meso-scale eddies of the Leeuwin Current on larval fishes.

North-west Shelf

The headwaters of the Leeuwin Current include the area off the north-west of Australia (D'Adamo *et al.* 2009). In this region, distributional patterns of larval fishes along two transects extending across the continental shelf near Dampier and to the east of Port Hedland (Figure 1) were described by Young *et al.* (1986). Although the results were somewhat confounded by use of different sampling gears between cruises, they noted a major discontinuity in larval fish composition just inshore of the shelf break. In general, larvae of fishes found as adults on the continental slope and open ocean characterised the deeper sampling sites (*e.g.*, Myctophidae, Gonostomatidae, Gempylidae, and Coryphaenidae) whilst larvae of species that were shelf-dwelling as adults (*e.g.*, Clupeiodei, Gobiidae, Carangidae, Apogonidae, Synodontidae and Lutjanidae) typified the shelf sites.

Further to the west, along a cross-shelf transect of stations in Exmouth Gulf that extended out past the Muiron Islands into the Leeuwin Current (15–75 m

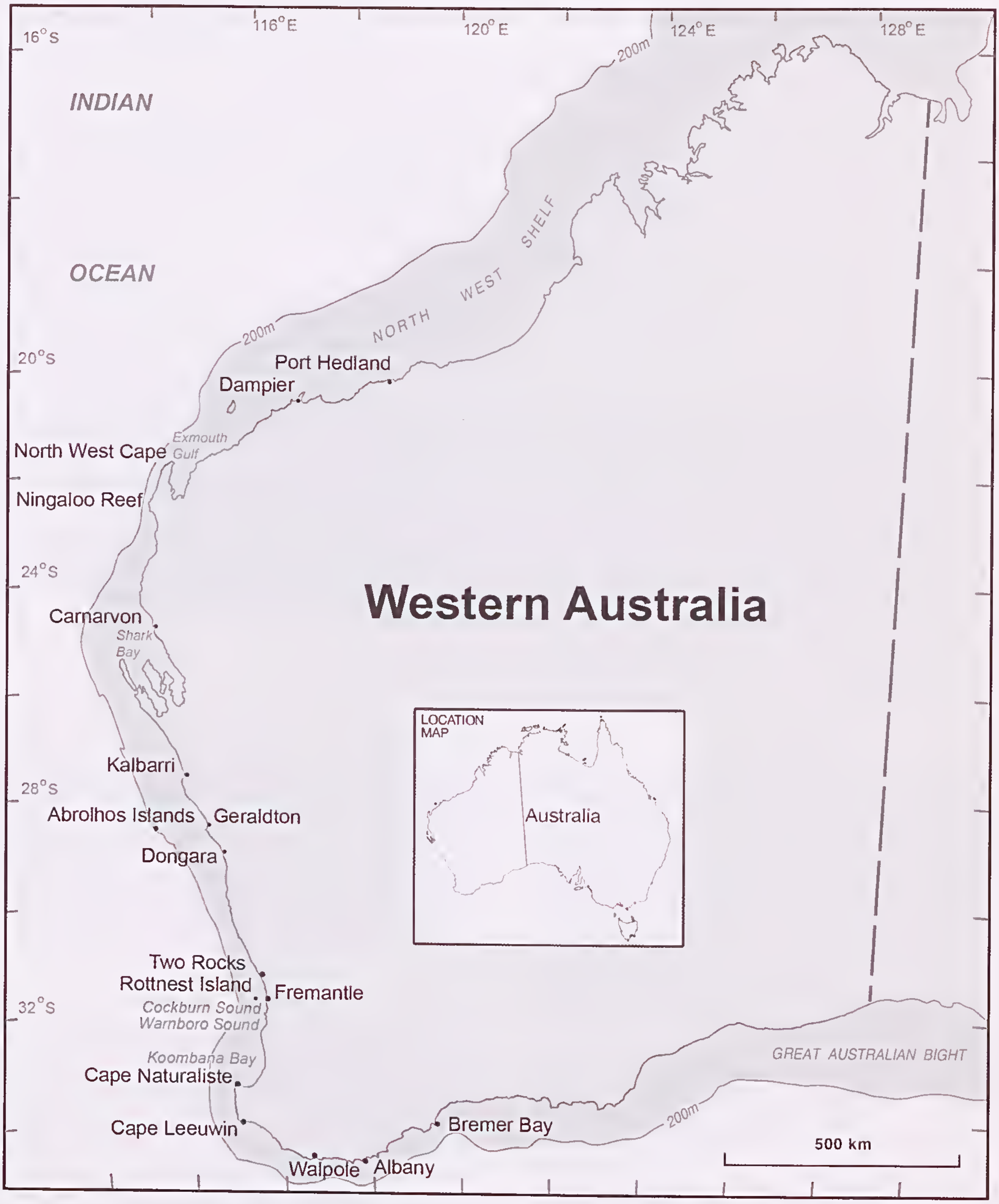

Figure 1. Map of Western Australia showing coastal localities mentioned in the text where studies of larval fishes have been completed.

depth), studies using light traps and plankton nets have been conducted during the austral summer months (Meekan *et al.* 2001, 2003; Sampey *et al.* 2004). The light trap work focused on comparing the catches between two light trap designs and between drifting and moored traps (Meekan *et al.* 2001). Catches in drifting traps were dominated by post-flexion larvae of reef fishes (*e.g.*, Pomancentridae, Blenniidae, Lethrinidae) whilst the moored traps caught predominantly Clupeidae. Despite differences in catch rates, multivariate analysis showed that cross-shelf patterns in catches were mapped equally well by both trap designs and Bray-Curtis classification analyses essentially split the inshore and mid-shelf stations from those stations further offshore. Larval fishes from bongo net tows conducted at one station in Exmouth Gulf (20 m depth) and another at 100 m depth west of the Muiron Islands were compared by Sampey *et al.* (2004). Although families such as Monocanthidae were more abundant at the inshore site, and Scombridae and Myctophidae were more abundant at the offshore site, they only discerned a weak cross-shelf pattern in the ichthyoplankton. This could probably be explained by the well-mixed water column at both stations and no evidence of lower salinity Leeuwin Current water at the deeper station.

At Ningaloo Reef, where the shelf is narrow and the inshore Ningaloo Current flows counter to the Leeuwin Current in summer (Woo *et al.* 2006; Hanson *et al.* 2007), flux of larval fishes across the crest of the reef during the summer months was examined by McIlwain (1997, 2002, 2003). Most of the larvae making the transition from the pelagic environment to the reef lagoon arrived during November and December. Time series analysis showed that semi-lunar periodicity was the most common pattern in larval supply, particularly for the abundant Blenniidae, Labridae, Synodontidae and Scorpaenidae which arrived on a 15 day cycle. Eel leptocephalii showed the strongest evidence of lunar cycling and the replenishment of Soleidae and Lethrinidae was also on a monthly basis. However, many larvae appeared to arrive completely stochastically. Cross-correlation techniques were used to compare differences in abundance at spatial scales of 500 m and 5 km and multi-specific patches of larvae at least 5 km wide were found to cross the reef crest into the lagoon habitat. The timing of these patches was often chaotic and rarely lasted longer than 24 h.

In summary, studies on larval fishes off the north-west region of WA are few and, with the exception of Young *et al.* (1986), they have only taken place in the summer months which is the time of weakest Leeuwin Current flow (D'Adamo *et al.* 2009). Nevertheless, offshore larval fish assemblages in Leeuwin Current headwaters appear to have distinctly different larval fish assemblages from those inshore on the shelf.

West coast

The marine ichthyoplankton assemblages off the west coast of Australia from Ningaloo to Cape Leeuwin remain poorly studied although some sampling programmes that focused on particular teleost species of commercial importance have been conducted by the WA Department of Fisheries. Gaughan & Mitchell (2000) investigated the biology of the tropical sardine (*Sardinella lemuru*) and this included enumeration of the eggs and larvae of this species from plankton samples collected across the shelf between Shark Bay and Dongara and out to the Abrolhos Islands. Summer spawning was confirmed and eggs were typically found over the outer half of the continental shelf. Although the influence of the Leeuwin Current was explored, they concluded that northward transport of early life history stages was more likely under the influence of the strong southerly winds that prevail during the summer months.

Numerical modelling of the dispersal of *Pagrus auratus* (pink snapper) eggs and larvae in Shark Bay (Nahas *et al.* 2003) concluded that the Leeuwin Current has a negligible influence on recruitment in gulf snapper populations and tides are the primary transport mechanism. The foraging ecology of five species of terns at the Abrolhos Islands has provided insight into larval fishes off the mid-West coast (Surman & Wooller 2003). They showed that the neustonic larvae of *Gonorhynchus greyii* (beaked salmon) and *Parupeneus signatus* (goatfish) were particularly important in the diet of lesser and brown noddies and sooty and roseate terns which foraged seaward of the islands in the vicinity of the Leeuwin Current.

Vertical and surface tows for plankton were conducted at 65 stations in shelf and slope waters between Fremantle and Exmouth by the Department of Fisheries in March 1996 (D Gaughan unpublished data). During two subsequent oceanographic cruises, CSIRO collected zooplankton samples using bongo nets along transects from North West Cape to the Abrolhos Islands in November 2000 and the Abrolhos Islands to Fremantle in October/November 2003 (J A Koslow unpublished data). Extraction of the fish larvae from these plankton samples was undertaken to try and locate the elusive larvae of tailor (*Pomatomus saltatrix*). Although very few tailor larvae were recorded from these samples (only six specimens from surface tows around Geraldton in March 1996), there was a clear trend of overall larval fish concentrations declining across the shelf and slope (Chisholm 2004). Some tailor larvae were extracted from surface plankton tows conducted around Rottnest Island by the Department of Fisheries in May 1999 (Chisholm 2004).

There were numerous, and extensive, surveys by the Department of Fisheries for the eggs and larvae of the commercially important sardine (*Sardinops sagax*) in shelf waters of the lower west coast over the period 1993–2004 (Fletcher *et al.* 1996; Gaughan *et al.* 2004, 2007). Muhling *et al.* (2008a) synthesised the data on the temporal and spatial distributions of sardine eggs and larvae off the south-western coast between Two Rocks and Cape Naturaliste and related them to the gonadosomatic index of adult sardines, daily growth rates of larvae and regional biological oceanography. While gonadosomatic index data suggested a distinct winter peak in sardine spawning activity, coincident with maximum seasonal surface chlorophyll concentrations, egg and larval distributions were not significantly higher in winter. This is likely due to the poor retention conditions for pelagic eggs and larvae on the mid-outer shelf during winter, as a result of the strength and location of the Leeuwin Current. Growth rates of larval sardines were unexpectedly high, averaging 0.70–0.89mm day^{-1} possibly because of the warmer water of the Leeuwin Current impinging on the shelf (Jones 2006; Muhling *et al.* 2008). Nevertheless, it was suggested that the coincidental timing of the modest seasonal maximum in primary productivity with the least favourable conditions for retention of pelagic larvae further compounds the restricted size of the sardine stock off south-western Australia.

Plankton samples taken over the continental shelf between Perth and Busselton confirmed that eggs and larvae of whitebait (*Hyperlophus vittatus*) occur primarily in shallow inner-shelf waters such as Cockburn Sound, Warbro Sound and Koombana Bay particularly in the winter months (Gaughan *et al.* 1996a,b). Studies conducted on the ichthyoplankton assemblages of the confined waters of Cockburn Sound (Jonker 1993; Kendrick 1993) and the Swan Estuary (Gaughan *et al.*

1990; Neira *et al.* 1992) revealed no evidence of any Leeuwin Current influence and the assemblages were dominated by larvae of teleosts found in temperate coastal waters.

SRFME programme

The Strategic Research Fund for the Marine Environment programme included the first detailed study of the biophysical oceanography off south-western Australia. This study focused on a transect extending offshore from Two Rocks (north of Perth) and, in addition to physical oceanography, covered nutrients, primary production, zooplankton and larval fish studies (Koslow *et al.* 2006, 2008; Muhling 2006). Muhling *et al.* (2008b) described the larval fish assemblages from inshore (18 m depth) to offshore waters (1000 m depth) off Two Rocks over a two and a half year period, and have related assemblage structure to oceanography. Assemblages showed strong spatial and temporal structure, which was well correlated to seasonality in water masses (Figure 2). The strength and position of both the Leeuwin and Capes Currents influenced variability in the marine environment, and, consequently, larval fish assemblages. In particular, the shoreward intrusion of the Leeuwin Current over the continental shelf in winter results in higher connectivity across the shelf, and greater similarity in larval fish assemblages between shelf and offshore waters, whereas in summer, larval fish assemblages were distinct between shelf and offshore stations.

Larval fish assemblages near the coast typically comprised larvae of inshore reef families, such as Blenniidae, Gobiidae and Monacanthidae. Shelf stations were dominated by larvae of pelagic families, such as Clupeidae, with *Sardinops sagax* and *Etrumeus teres* the most abundant species within this family. In summer, Labridae larvae were also abundant over the shelf, whereas in winter, larvae of oceanic fishes from the Myctophidae (*e.g., Diogenichthys atlanticus*) and Phosichthyidae (mostly *Vinciguerria* spp.) were more abundant. Seaward of the shelf break, the larval fish assemblage was dominated by oceanic larvae throughout the year, with only slight seasonal changes in species composition. Some vagrant, tropical larvae, such as Pomacentridae and Ostraciidae were collected at stations on the outer shelf and slope during summer and autumn, within the southward flow of the Leeuwin Current.

Larval fish assemblages from within the Leeuwin Current generally had similar species, however, assemblages from shelf stations inundated by the Leeuwin Current were distinct from those taken in the core of the Leeuwin Current (Muhling *et al.* 2008b). This suggests that water depth and/or distance from shore has a structuring effect on assemblages not completely related to water mass and probably reflects differing spawning locations of the diverse species assemblage of fishes in south-western Australia.

Seasonal variability in cross-shelf transport, and thus larval fish assemblages, was investigated by Muhling & Beckley (2007). The horizontal and vertical distributions of larvae across the shelf and offshore were found to be strongly influenced by the current regime at the time of sampling. A winter cruise in August 2003 was undertaken during a time of strong, southward Leeuwin Current flow, while the northward flowing Capes Current, in combination with surface offshore Ekman transport, predominated during the summer cruise of January 2004. The southward flow of the Leeuwin Current extended to >150 m depth during winter, effectively limiting any retention of larvae on the shelf at

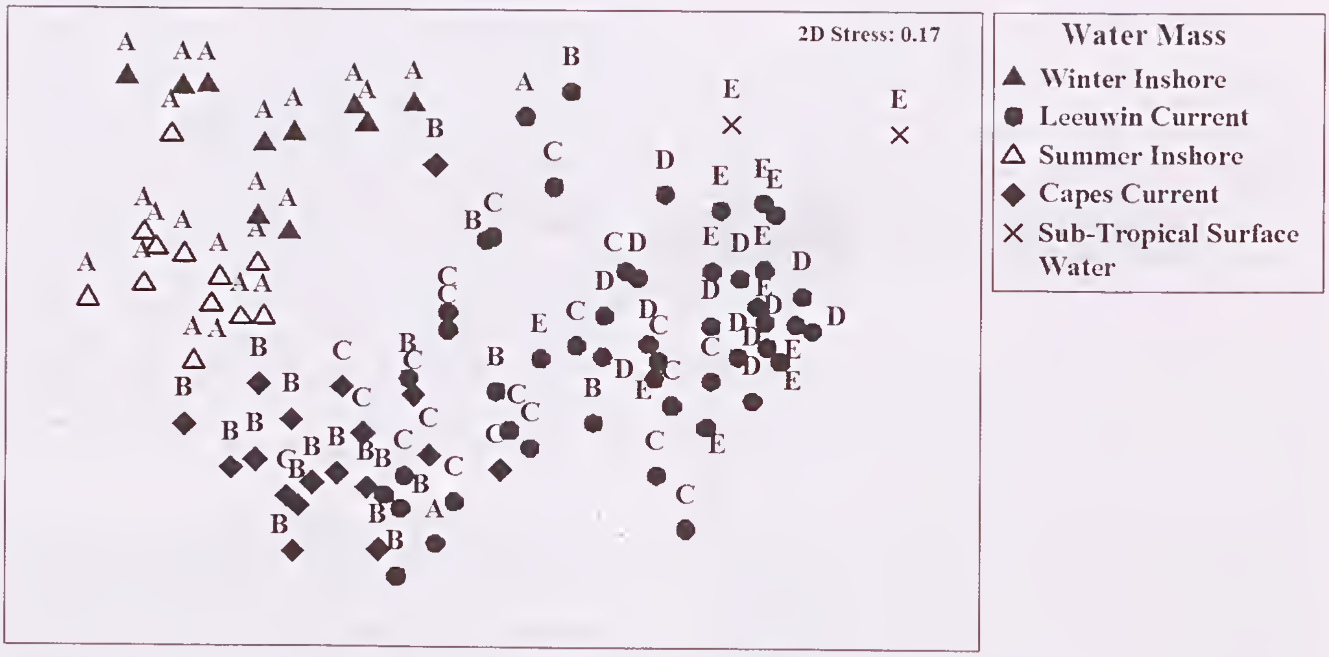

Figure 2. Multi-dimensional scaling ordination of larval fish assemblages and water masses along the Two Rocks SRFME transect across the shelf and Leeuwin Current off south-western Australia (2002–2004). Stations were at 18 m (A), 40 m (B), 100 m (C), 300 m (D) and 1000 m (E) depths.

this time. These factors, in combination with the vertical depth preferences of larvae of different taxa, largely determined their distribution patterns. A conceptual model of larval fish assemblages in relation to water masses off the lower West coast is given in Figure 3.

Leeuwin Current eddies

Meso-scale eddies are conspicuous features of the Leeuwin Current (Cresswell & Griffin 2004) and a dedicated, multi-disciplinary cruise to examine the oceanography and ecology of a pair of counter-rotating eddies off south-western Australia was conducted in October 2003 (Waite *et al.* 2007a; Feng *et al.* 2007). Muhling *et al.* (2007) examined the larval fish assemblages in both the cold-core, cyclonic eddy and the warm-core, anticyclonic eddy which had propagated seaward from the shelf edge. Despite the warm-core eddy being characterized by coastal diatoms (Thompson *et al.* 2007; Waite *et al.* 2007b), larval fishes in both eddies were dominated by oceanic families such as Myctophidae, Phosichthyidae, Gonostomatidae, Sternoptychidae, Paralepididae and Stomiidae. However, larval fish assemblages from the warm-core eddy were significantly different from those in the cold-core eddy. Larval fish assemblages were more variable within the warm-core eddy, both across eddy zones (centre, body and perimeter) and within depth strata, than in the cold-core eddy. Depth of the mixed layer was strongly correlated with assemblages in the warm-core eddy but not in the cold-core eddy. Stable isotope analysis (Waite *et al.* 2007c) suggested that larval fishes in the warm-core eddy were preferentially targeting food sources derived from large phytoplankton carbon such as that found in the diatoms of the warm-core eddy.

Pelagic larval duration among coastal fish species is typically a few weeks (MacPherson & Raventos 2006). Thus, as the eddies studied by Muhling *et al.* (2007) were located 300–600 km offshore and were already 4–5 months old when sampled, it was not possible to ascertain the influence of the eddies in entraining coastal fish larvae off the shelf. Gaughan (2007) hypothesised on potential influences of Leeuwin Current eddies on teleost

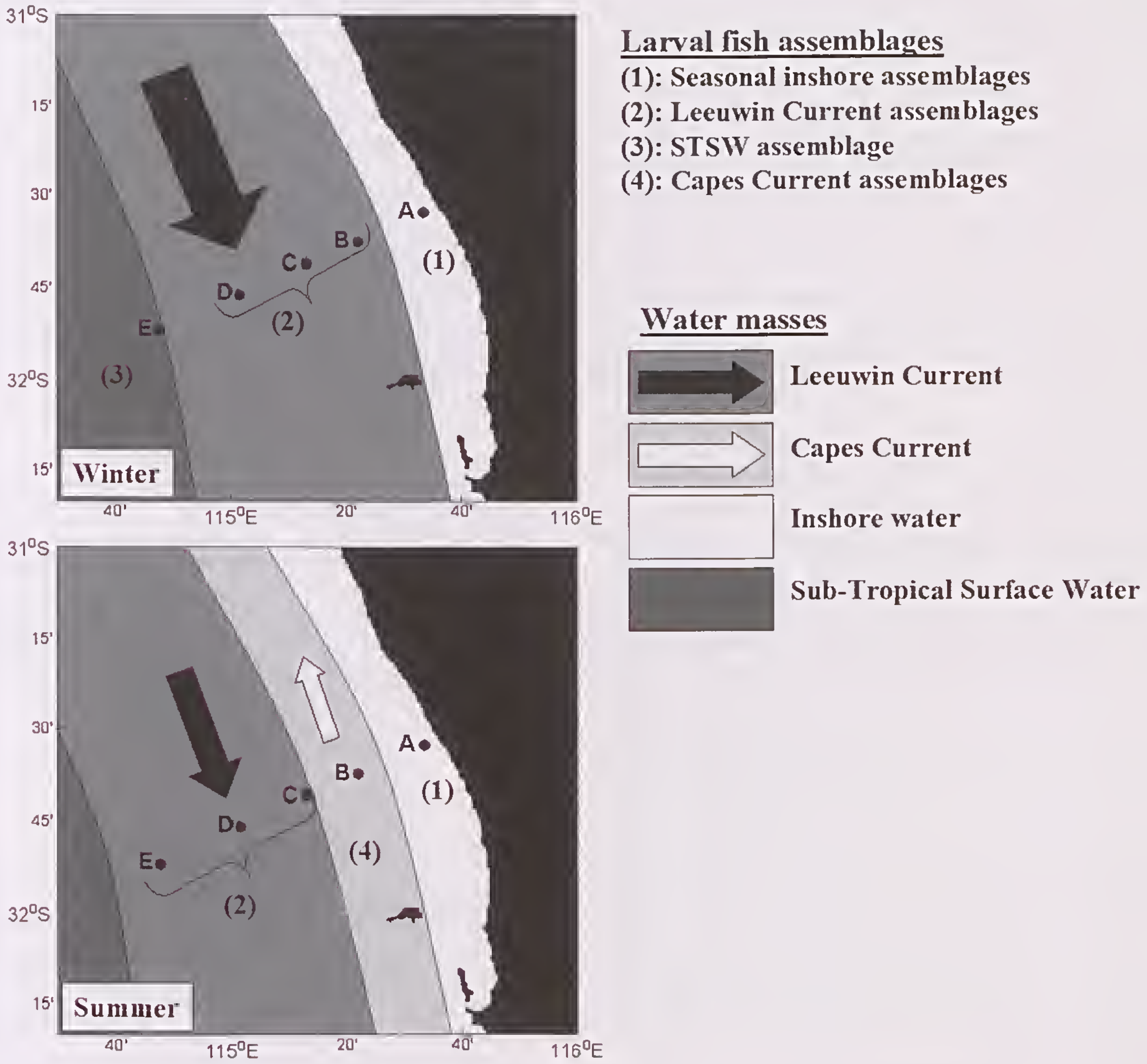

Figure 3. Conceptual diagram indicating seasonality in water masses and associated larval fish assemblages off the lower west coast of Australia.

recruitment to the Western Australian continental shelf suggesting that retention/loss of teleost eggs and larvae and positive/negative influences on feeding conditions for larvae were of importance.

South coast

Along the south coast of WA, ichthyoplankton studies have focused on eggs and larvae of sardines (*Sardinops sagax*). Fletcher & Tregonning (1992) sampled out to the edge of the continental shelf off Albany and concluded that most spawning of sardines was inshore of the main influence of the Leeuwin Current. They found peaks in egg abundance in both July and December but only a December peak in larval abundance and speculated that this could reflect higher larval transport out of the study area in winter when the Leeuwin Current was strongest.

In a subsequent study, Fletcher *et al.* (1994) examined inter-seasonal variation in the transport of sardine eggs and larvae over the continental shelf along the south coast from Walpole to Bremer Bay by using a fleet of fishing vessels to sample the area over as short a time period as possible. They concluded that, during winter, the location of the Leeuwin Current had a direct effect on spawning as eggs were most abundant off Albany in a band of cooler coastal water and there were very few to the west where the Leeuwin Current was close to the coast. Larvae were distributed further to the east with highest numbers towards Bremer Bay. They determined that the consistent shifts in the abundance peaks of the different egg and larval stages indicated drift of 30–40 km d^{-1} corresponding to an easterly flowing current speed of 0.3–0.46 m s^{-1}. In summer, all stages of eggs and larvae were distributed throughout the study area with the peak in abundance on the shelf off Albany and there was no obvious local oceanographic influence on their abundance as the Leeuwin Current had weakened near Cape Leeuwin.

Using geo-statistical techniques, Fletcher & Sumner (1999) examined the fine scale spatial distribution of sardine eggs and larvae of various ages off Albany. They showed that sardine eggs have a patchy distribution which reflects the spawning behaviour of adults. For older larval stages, patch size increased and the level of cohesion decreased. Various studies to investigate aspects of sardine larval ecology were conducted during a research cruise from Adelaide to Albany across the Great Australian Bight in July 1994. Using a multiple opening and closing EZ net, Fletcher (1999) showed that recently spawned eggs were generally located in 40–60 m of water and that larvae were near the surface though during the night they tended to be slightly deeper in the water column (15–30 m). During this study an attempt was made to document the larval distributions of other selected fishes found during surface and vertical tows. The neustonic larvae of *Scombersox saurus, Cheilodactylus* sp. and *Gonorhyncus greyii* were most abundant on the shelf-edge and slope whilst larvae of neritic Labridae, *Scomber australasicus* and *Etrumeus teres* were most abundant on the shelf between Albany and Bremer Bay (Fletcher *et al.* 1996).

Gaughan *et al.* (2001a) determined the growth rate of *S. sagax* larvae from samples collected during this cruise across the Great Australian Bight and found the mean growth rate to be 0.48 mm d^{-1}. As indicated in their comparative table this value is less than that found for sardine larvae in other parts of the world. They concluded that the lower productivity off the oligotrophic south coast, partly induced by the Leeuwin Current, was responsible for this low growth rate.

The potential for transport of larval sardines between Western Australian and South Australian fishery management areas was assessed by examining the eastward movement of surface water and the age and hatch-date distributions of larvae in shelf waters across the Great Australian Bight (Gaughan *et al.* 2001b). Generally, the ages of larvae tended to increase from west to east but the mean estimated flow on the shelf of 0.1 m s^{-1} (calculated from ADCP and wind data during the cruise) was insufficient to support the hypothesis that larvae could passively advect from Western Australia to the eastern Great Australian Bight. However, the Leeuwin Current was particularly weak during the year of the study, and the authors contended that potential links between distant areas through larval dispersal requires consideration especially with regard to the scale of fisheries management units. Similarly, Dimmlich *et al.* (2000) explored the transport of larvae of Australian herring (*Arripis georgianus*) from WA where they spawn (Fairclough *et al.* 2000) to South Australia using a transport model incorporating wind-generated coastal currents and the Leeuwin Current. They concluded that in years of stronger transport, recruitment to South Australia was higher.

The results from numerous Department of Fisheries plankton surveys for sardine eggs that took place periodically between 1991 and 2005, and covered much of the southern coast of Western Australia, have allowed examination of the re-growth of sardine stocks following the mass mortality event of 1998/99 as a result of a widespread epizootic infection (Gaughan *et al.* 2004, 2007). Using the daily egg production method, estimates of spawning biomass, from before and after the epidemic, were integrated into an age-structured simulation model. The simulation model utilized information on factors that increase (*e.g.*, recruitment, growth rate) and decrease (*i.e.*, mortality due to fishing and natural causes) stock size to estimate changes in biomass over time. The analyses showed a strong recovery of sardine stocks in WA from the very low levels that remained after the mass mortality event of 1998/99.

Further research

At present there is considerable research effort being focused on the biological oceanography of Leeuwin Current eddies, in particular, the cross-shelf transport of larval fishes during the formation of eddies (Holliday & Beckley unpublished data). A four-week cruise was conducted in May 2006 and covered the area 30–34°S and westward from the coast to 112°E (Paterson *et al.* 2008). Vertical distribution patterns of larval fishes derived from depth-stratified sampling using an EZ net during this cruise combined with concurrent ADCP data and drifter tracks are being used to examine this process.

In May/June 2007, an intensive study of the biological oceanography of the Leeuwin Current was undertaken and included sampling across the shelf and slope out to a depth of 2000 m along transect lines at each degree of latitude from 34°S (Cape Leeuwin) to 22ºS (North West Cape) (Thompson *et al.* unpublished data). Along these transects, zooplankton and neuston samples were collected in oceanic, Leeuwin Current and shelf waters for elucidation of the larval fish assemblages (Beckley *et al.* unpublished data). This study took place during the autumnal increase in Leeuwin Current strength and primary production on the shelf (Lourey *et al.* 2006) and a repeat cruise during summer months when Leeuwin Current flow is weaker would provide an interesting contrast.

Identification of larval fishes requires the existence of appropriate descriptions of the larval stages. Larvae of widely distributed oceanic fishes have been relatively well described in the international literature and many of these publications can be used to identify those occurring in the Leeuwin Current (*e.g.*, Moser *et al.* 1984; Olivar *et al.* 1999; Richards 2006). Similarly, the major treatise by Leis & Carson-Ewart (2000) is particularly useful for identification of the larvae of Indo-Pacific tropical fishes entrained in the Leeuwin Current. Larvae of many temperate Western Australian coastal fishes, especially those of commercially important species, are included in the volume by Neira *et al.* (1998). However, for some of the speciose inshore families (*e.g.*, Labridae) lack of appropriate larval descriptions makes resolution to species level extremely difficult. This is somewhat of an impediment to studies on the influence on larval fish ecology of oceanographic processes associated with the Leeuwin Current and inshore counter currents (*e.g.*, Capes Current) which appear to be important in retention of the larvae of coastal species spawning in the summer months.

Conclusion

In essence, larval fishes assemblages of the Leeuwin Current comprise a mixture of oceanic, slope, tropical and temperate coastal species, reflecting both the source waters and advection into the current on its 5 000 km-long trajectory around WA. Seasonality in strength and location of the Leeuwin Current appears to have a profound effect on the ecology of larval fishes in the region. There is considerable scope for investigations into the ecological processes associated with the Leeuwin Current as well as seasonal, inshore counter currents along the WA coast.

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The ongoing influence of the Leeuwin Current on economically important fish and invertebrates off temperate Western Australia – has it changed?

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Abstract

Earlier reviews have identified that the strength of the Leeuwin Current is a key factor associated with changing abundance of a number of key invertebrate and scalefish species harvested by on-shelf commercial fisheries off the Western Australian coast. This review of these relationships has revealed that the addition of more recent data has strengthened the relationship for western rock lobster, the only species whose larvae are primarily distributed in the area of the influence of the Leeuwin Current and its offshore eddies. For other species, particularly scallops and whitebait, while the addition of new data has weakened the LC relationships, other as yet unquantifiable factors now appear to be more important determinants of changing abundance. For a number of the scalefish species (*e.g.*, south coast Australian salmon), discontinuation of juvenile monitoring and the lack of ongoing records of comparable abundance data, primarily as a consequence of changes in the distribution of fishing, relative to the distribution of the stocks, has precluded ongoing exploration of earlier relationships. However preliminary data for some hitherto unreported relationships for other coastal scalefish species suggest that some physical and biological variables that are likely to be influenced by both the Leeuwin and Capes Currents may also be important. To help unravel these relationships, the underlying mechanism of the influence of the current, particularly the role of the northward flowing, mid-shelf Capes Current and salinity of shelf waters, and factors controlling the availability of nutrients to on-shelf primary productivity need to be better understood.

Keywords: Leeuwin Current, invertebrates abundance, scalefish abundance, time-series robustness

Introduction

The Leeuwin Current (LC) is a poleward flowing eastern boundary current that carries warm, low salinity water southward along the shelf break off the Western Australian (WA) coast (Cresswell & Golding 1980; Waite *et al.* 2007).

Mesoscale interannual and seasonal variability in the LC strength (Ridgeway & Condie, 2004), measured as coastal sea level height, has been shown to be related to the El Nino/Southern Oscillation (ENSO) cycle, with LC strength highly correlated with the Southern Oscillation Index (SOI); the current being weaker during ENSO events and stronger during La Nina events (Pearce & Phillips 1988, Caputi *et al.* 1996, Feng *et al.* 2003). While the LC strength is also correlated with temperature and salinity of outer shelf waters, air-sea heat flux processes rather than advection associated with the LC appear to be the key factors influencing the temperature and salinity of shallower coastal waters inshore of the current (Pearce *et al.* 2006).

Earlier reviews (Lenanton *et al.* 1991; Caputi *et al.* 1996; Pearce *et al.* 1998) have revealed that LC strength was correlated with the abundance and/or catchability of a number of target species taken in a range of on-shelf commercial fisheries off the coast of South-Western Australia (SWA) (Figure 1). For most of these species there are long-term data bases that either measure the abundance of settlement life history stages, or the abundance of adults. They include western rock lobster (WRL, *Panulirus cygnus*), Shark Bay scallops (*Amusium balloti*), Shark Bay king prawns (*Penaeus latisulcatus*), Australian salmon (*Arripis truttaceus*), Australian herring (*Arripis georgianus*), Albany pilchards (*Sardinops sagax neopilchardus*), and whitebait (*Hyperlophus vittatus*). All of these relationships with the LC strength were "invoked" from statistical correlations; they can be either positive (*e.g.* western rock lobster), or negative (*e.g.* Shark Bay scallops). Few of the underlying mechanisms have been empirically verified, although the timing of the period when the current affected the stock indicated that in most instances, the larval phase appeared to be the main life history stage influenced by the current. For example, the contention by Fletcher *et al.* (1994) that "loss" of larvae due to the LC reduces recruitment of pilchards two years later was supported by Gaughan *et al.* (2001) who found that the larvae of south coast pilchards could be transported up to 1000 km east, and in some cases well into South Australian waters, primarily under the influence of the LC. Increases in availability and resolution of oceanographic data (*e.g.* satellite derived steric height data to derive surface current patterns) have permitted advances in modeling of potential transport of the larval stages of WRL. However, there have been no

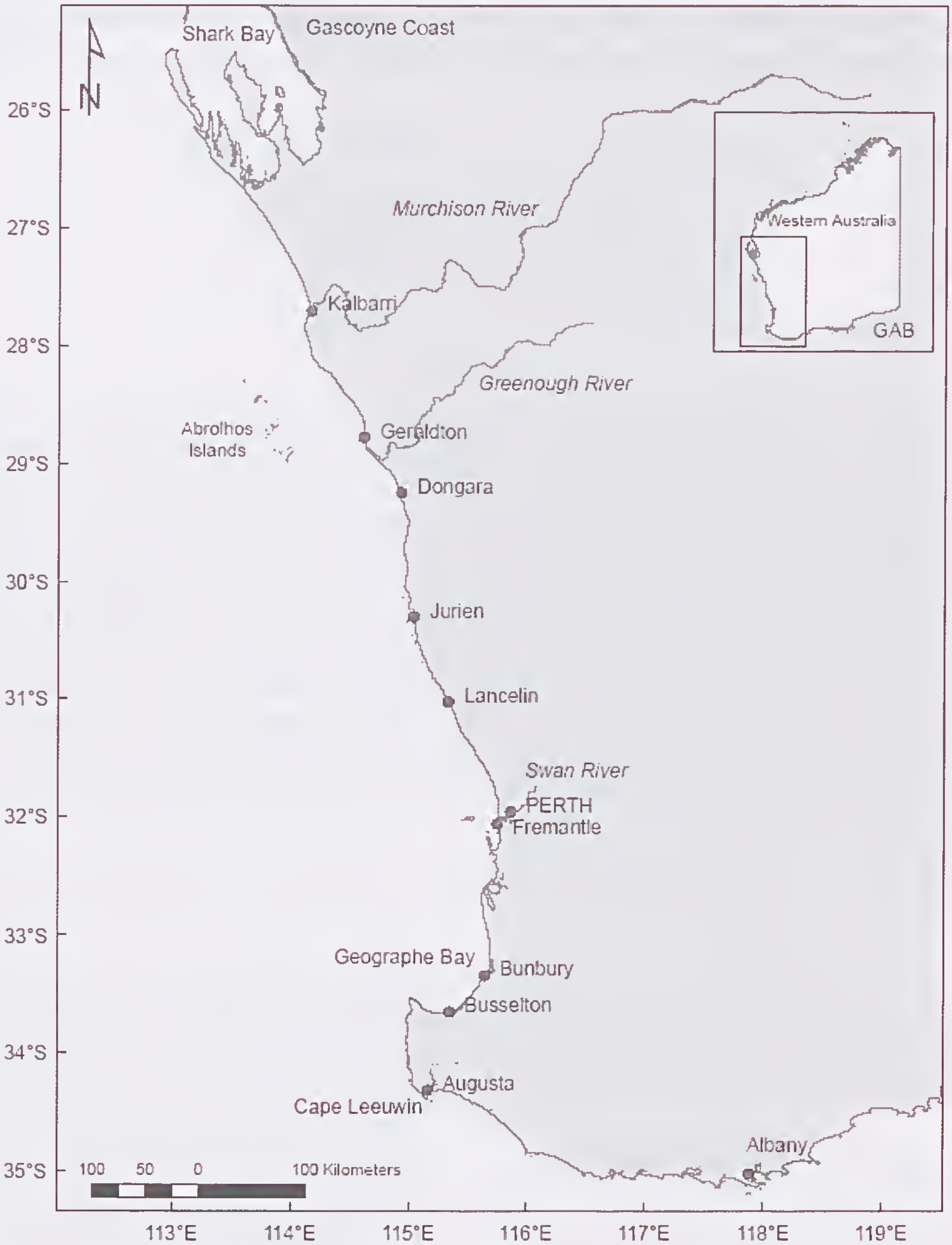

Figure 1. Key locations along the lower west and western south coasts of Western Australia.

other studies directed at determining the influence of oceanographic variability on transport or survival of the larval stages of marine species.

Ongoing research during the 30 years since the formal recognition of the existence of the LC (Golding & Symonds 1978; Cresswell & Golding 1980) has revealed that this surface flowing current is one of four major currents that comprise the Leeuwin Current System (LCS) (Batteen *et al.* 2007). Beneath the southerly surface-flowing LC, the Leeuwin Undercurrent (LUC) flows northward in subsurface waters, while the wind generated Capes and Ningaloo Currents flow respectively northward on the shelf shoreward of the LC off the lower west coast, and the Gascoyne coast, during the austral summer. Mesoscale features such as eddies and meanders are also associated with the LCS. The way in which this system influences the water column behaviour and biological productivity off the WA coast has recently been reviewed in greater detail (Waite *et al.* 2007). In addition to the LCS, global atmospheric changes are also contributing to the observed long-term temperature and salinity changes to continental shelf waters off Western Australia (Pearce & Feng 2007). However, as noted above, while such changes are acknowledged as factors that may further influence the complex interrelationships between the LCS and fisheries production, indices of such changes are broad, making it inherently difficult to empirically demonstrate conclusive causal relationships; something few studies undertaken thus far have been able to achieve. Given this dearth of studies focused on determining causal relationships, the aim of this paper is to review the ongoing robustness of the hitherto established relationships between interannual and seasonal variability in LC strength and species abundance in the regions of relevance to fisheries (*i.e.* fisheries production or recruitment), and highlight any further examples where the abundance of economically important species is being influenced by the LCS.

This review updates the previous assessments from earlier reviews, either building on hypotheses identified earlier or invoking plausible conceptualizations of causal links between the LC and species abundance. In the absence of information that can be used directly to ascribe mechanisms of influence, such hypotheses are framed around physical and biological effects linked to variability in the LCS and which may affect different life history stages of the various species. Physical effects could be changes in temperature to levels sub-optimal for growth, or transport of eggs or larvae (Muhling & Beckley 2007; Muhling *et al.* 2008a). Biological effects could include changes to nutrient regimes and broader patterns of primary productivity leading to variability in growth and survival.

Data sources

The relationships between 10 species/fisheries and the LCS are reviewed here, building on the seven covered in earlier reviews (Lenanton *et al.* 1991; Caputi *et al.* 1996). Details of the biological data used here, such as method of collection and any validations undertaken, are not dealt with here unless explicitly relevant. Rather, the pertinent data are mentioned as required to build the conceptual understandings and hypotheses relevant to progressing our knowledge of how the LCS affects fisheries production off the WA coast.

For each species or fishery the primary historical data consists of commercial catch and effort records, typically available since 1975. These compulsory catch and effort data are aggregated monthly by fishing method for each one degree by one-degree block (or to other spatial fishing zones for some fisheries), submitted to the Department of Fisheries, and stored in the Catch and Effort System (CAES) database.

The fisheries/species covered in this review are shown below. Further details of these fisheries can be found in the Department of Fisheries, Western Australia annual State of the Fisheries reports available from www.fish.wa.gov.au.

- western rock lobster (WRL, *Panulirus cygnus*)
- Shark Bay scallops (*Amusium balloti*)
- Shark Bay king prawns (*Penaeus latisulcatus*)
- Green or giant mud crabs (*Scylla serrata*) *
- Australian salmon (*Arripis truttaceus*)
- Australian herring (*Arripis georgianus*)
- Albany pilchards (*Sardinops sagax neopilchardus*)
- whitebait (*Hyperlophus vittatus*)
- tailor (*Pomatomus saltatrix*) *
- West Australian dhufish (*Glaucosoma hebraicum*) *

* species added since the last review.

Oceanography and meteorology

Below are the sources of monthly values of the physical variables that were used when exploring relationships with abundances indices of different species:

- Southern Oscillation Index (SOI): http:/ www.bom.gov.au/climate/current/soihtm.shtml);
- Fremantle Sea Level (FSL): National Tidal Centre in Adelaide;
- Sea surface temperatures (SST) on a 1° latitude/ longitude grid: Reynolds Global dataset (Reynolds & Smith 1994); and
- Rainfall: the Bureau of Meteorology (http:// www.bom.gov.au/silo/products/Rain.shtml).

Monthly at-sea measurements of surface and bottom salinity and temperature have been made at four locations, Fremantle, Lancelin, Jurien and Dongara, across four depths, <10, 10–20, 20–30, and >30 fm during the WRL fishing season (15 November to 30 June) each financial year since 1971/72 (Caputi *et al.* 2009; Lenanton *et al.* 2009).

Recruitment Indices

The tailor recruitment index was expressed as a catch rate, calculated as the average number of 0+ and 1+ yr old tailor caught per standard angling hour over the period February to April at a representative Perth Metropolitan site (Ayvazian *et al.* in prep.).

The dhufish recruitment index was derived from the current age structure, back-calculated to estimate the abundance of the each age cohort during the year of its birth (St John unpublished).

The Australian salmon recruitment index is the standardized catch rate of 0+ individuals settling in nursery areas off the lower west coast between September and December each year, and is derived from data collected during an ongoing coastal scalefish recruitment index survey (Gaughan *et al.* 2006).

Results and Discussion

Western Rock Lobster

While adults are confined to the shelf, larval stages are distributed throughout oceanic waters adjacent to the continental shelf off the coast of SWA (Phillips 1981). The final larval stage (puerulus) actively swims from oceanic waters across the shelf to settle in shallow coastal habitats. There are long-term databases recording indices of the annual abundance of settling puerulus, environmental variables such as LC strength (April Fremantle sea level), satellite derived sea surface temperature (SST February–April), and westerly wind during peak settlement (October to November)(rainfall index of storm fronts). Correlations using data since the

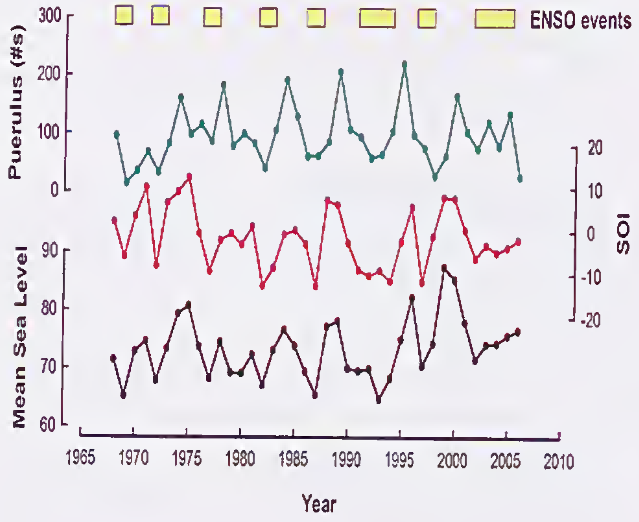

Figure 2. Annual mean values of the Southern Oscillation Index, Fremantle mean sea level, and puerulus settlement at Seven-Mile Beach Dongara Western Australia (Updated from Pearce and Phillips 1986).

late 1960s have revealed a strong positive relationship between puerulus settlement, mean Fremantle sea level and the SOI (Figure 2) (Pearce & Phillips 1988). Further, there is also a strong positive relationship between mean monthly SST (February to April) and puerulus settlement, with strongest settlement often occurring during years exhibiting high SST levels combined with the strongest rainfall index (*i.e.* periods of strongest westerly winds) (Figure 3).

It seems that in years of strong LC, the survival and growth of WRL early stage larvae is enhanced, either via retention of larvae in anticyclonic warm core eddies, and/or as a result of improved growth and survival as a consequence of warmer temperatures and/or higher productivity (chlorophyll A) during late autumn/winter. Potential sources of nutrients include upwelling associated with eddy formation, advection from the shallower nutricline further north, and seasonal cooling and storms which promotes convective mixing of the water column and shoaling of the nutricline (Koslow *et al.* 2008). Understanding the causal mechanism of the effect of the LC is an area of ongoing research.

Research has also demonstrated that strong LC in the second half of the year (June–December) which is near the period of peak settlement (August–December) has an advection effect as it distributes puerulus further south (Figure 4) (Caputi 2008).

Thus annual puerulus settlement (abundance), LC strength (Fremantle sea level), SST, productivity (chlorophyll A), and eddy kinetic energy are all positively correlated (Caputi *et al.* 2001; Feng *et al.* 2005), with the more southerly distribution of higher puerulus settlement also positively correlated with LC strength (Caputi 2008). However the frequency of ENSO events (weak LC) over the last 16 years (1991–2006) has been greater than in the previous 20 years (1971–1990). If this trend continues, is there likely to be a continuing trend in average to low puerulus settlement; or will the influence of global climate change (increasing SST of the WA coast, particularly the lower west coast) to some extent counter the negative influence of weak LC?

There has also been considerable effort expended exploring the effect of long-term temperature increases

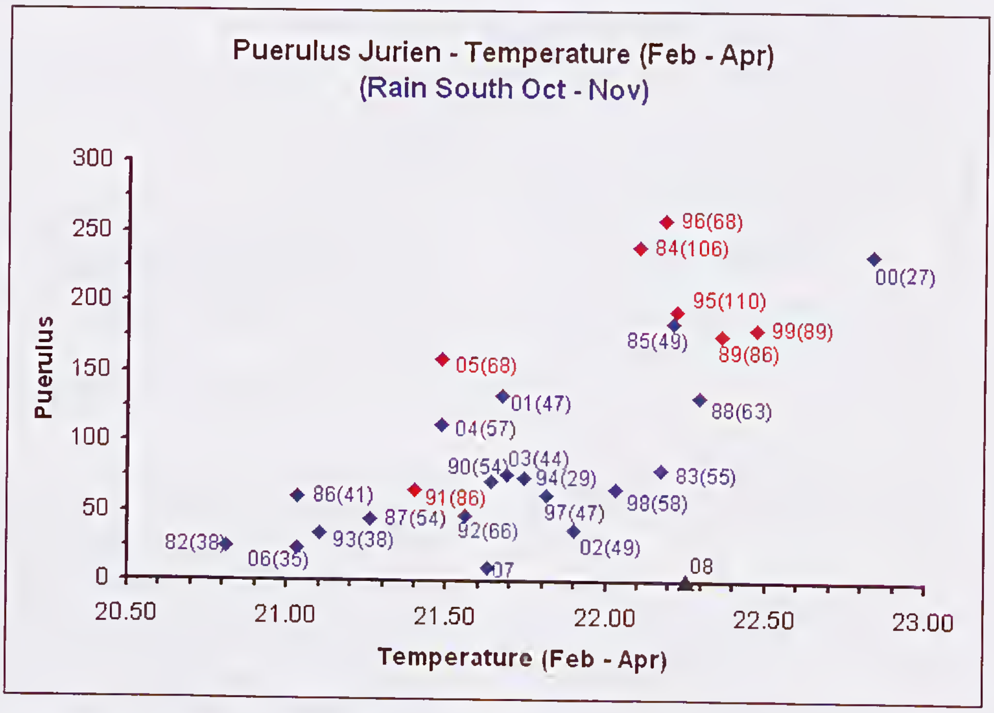

Figure 3. Relationship between the annual puerulus settlement (mean number per collector) at Jurien, and sea surface temperature, at two levels of rainfall (red data points >, and blue data points < than 80 mm, an index of the strength of westerly winds) in October–November, off the lower west coast of Western Australia (updated from Caputi *et al.* 1996). The predicted level of puerulus settlement for 2008 is presented. The multiple correlation is 0.82 (p<0.001) for 1982–2006 data.

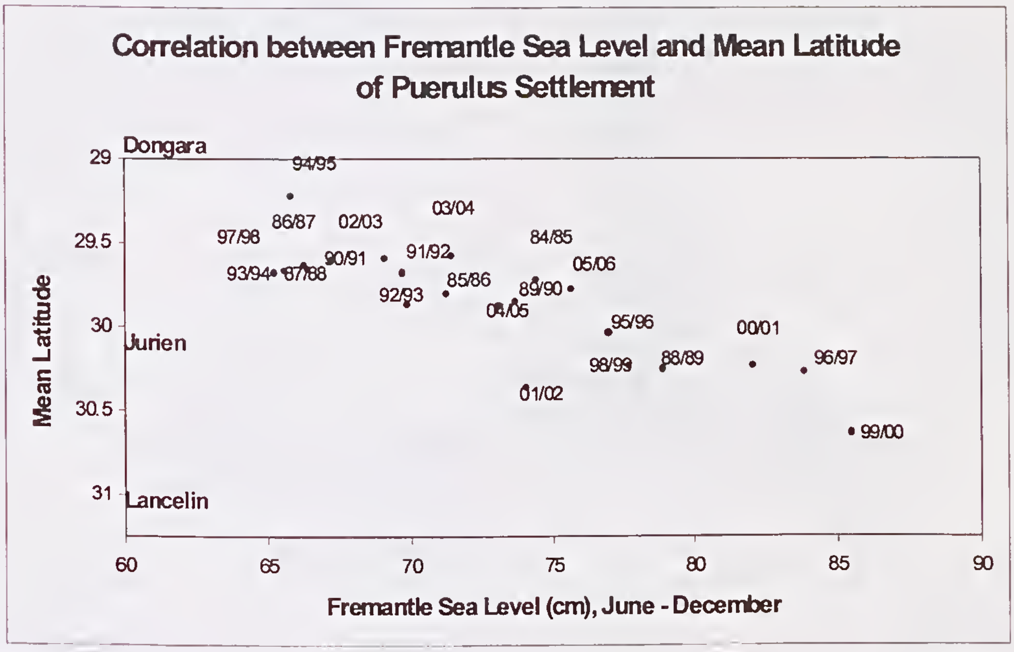

Figure 4. Relationship between the Leeuwin Current strength (measured by Fremantle sea level) over June to December, and the annual mean latitude of puerulus settlement at sites along the lower west coast of Western Australia (r=0.86, p<0.001 Caputi 2008).

(Pearce & Feng 2007) on growth, size at migration, size at maturity, catchability, and timing of moulting (thus peak catch rates) of WRL (Caputi *et al.* in prep.).

Scallops

Scallop recruitment is highly variable (Joll 1994; Joll & Caputi 1995). In WA, this is seen by widely varied annual commercial scallop catches in the main scallop fisheries, which occur at Shark Bay, the Abrolhos Island (Mid-west Trawl Fishery) and off the south coast (South Coast Trawl fishery). The Shark Bay scallop fishery has historically been the most productive fishery in WA, with annual catches ranging between 600 to 22,000 tonnes (whole weight). However, in 2003 and 2005 the Mid-West Trawl fishery recorded higher annual landings for scallops and in 2000 the South Coast Trawl fishery recorded the highest scallop catches in the state for that year (Figure 5).

Scallops are broadcast spawners (Kailola *et al.* 1993) with a larval duration of about two to three weeks (Rose *et al.* 1988). During this period larvae are susceptible to being passively transported by tides and currents whilst in the water column. Larval survival is affected by food availability and predator abundance, and the length of the larval period (assuming survival is enhanced by reducing time in the plankton community) can also be influenced by water temperature.

Annual scallop surveys, conducted between October and December, have been undertaken in Shark Bay since 1983, and provide size class and abundance information from over 90 trawl sites within the bay. These data are used to determine an index of recruitment strength during that year (individuals derived from the current years spawning) and provide the basis for predicting the catch the following year. They also provide an index of the size of the residual stock (older scallops remaining from the year before and possibly 2 years before, noting the life span is 2–3 years). For the Abrolhos Islands, a regular pre-season survey has also been undertaken in October since 1997, and as for Shark Bay, a catch prediction for the following season can be made using the survey abundance index derived from the pre-season survey.

The pattern of settlement in both Shark Bay and the Abrolhos Islands is variable between years and settlement patterns are patchier in the Abrolhos Islands compared to Shark Bay. The patchiness may reflect the habitat and/or the water current circulation pattern and eddies that occur at the Abrolhos Islands. However key areas where settlement may occur in any one year are now reasonably well known for both fisheries. No fishery independent surveys are conducted on the south coast. Normally in this region, one boat is elected to 'survey' potential settlement sites (derived using fishers knowledge) and if an encouraging "showing" of scallops is located, the other boats (only four licenses issued in the South Coast Trawl fishery) may elect to fish during the season.

Leeuwin Current correlation with recruitment of *Amusium balloti*

Shark Bay

In the 1980s in Shark Bay, a good correlation was observed between scallop recruitment strength and the strength of the Leeuwin Current (Joll & Caputi 1995). The proxy used for the LC is the height of the Fremantle Sea Level (FSL) during May to August, lagged by 1 month from the peak scallop spawning period of April to July to account for the latitudinal difference between Shark Bay and Fremantle. It was apparent that in years of weaker LC flow, higher recruitment success was observed and vice versa. A more recent analysis of LC

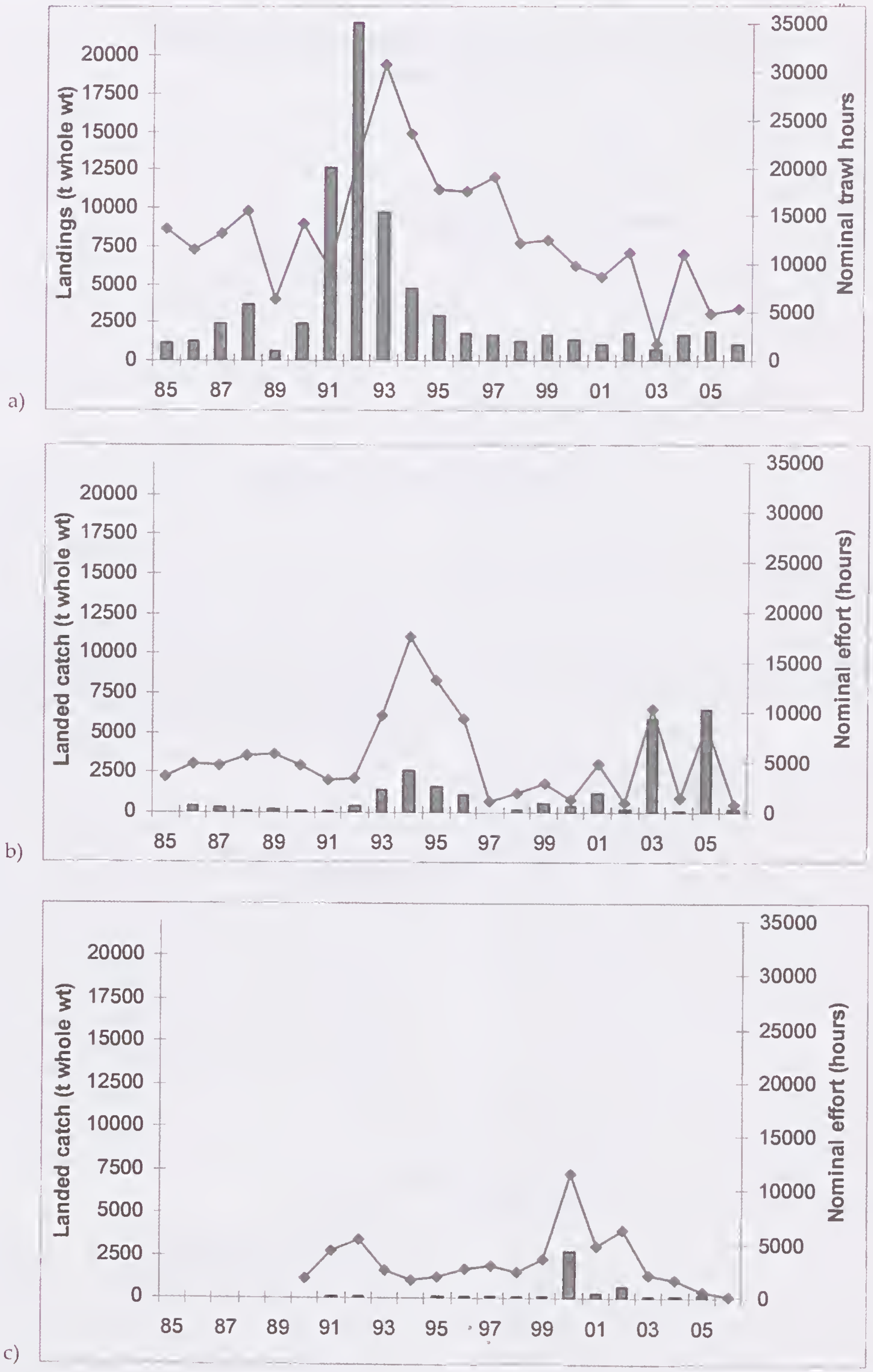

Figure 5. Annual scallop landings (tonnes whole weight – bar histograms) and nominal hours of trawling (line graph) in a) Shark Bay, b) Abrolhos Islands and c) South Coast trawl fisheries

strength and scallop recruitment in Shark Bay using data collected between 1983 and 2006 indicates a much weaker negative correlation (Figure 6) than the one reported for the 1980s. Similarly, a relatively weak negative correlation was observed between scallop recruitment and surface water temperature (Figure 7). There is some indication that a weak LC flow and/or cooler water temperatures benefit recruitment but not sufficient in themselves to always result in good recruitment. Other factors (*e.g.* water current movements during larval phase) must also be strongly influencing recruitment.

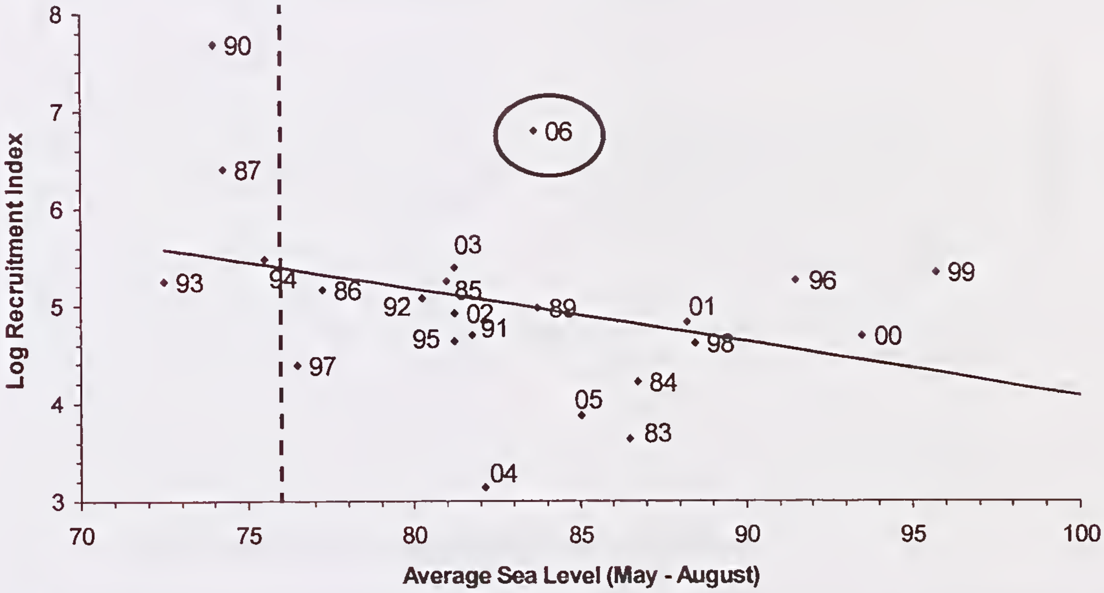

Figure 6. Correlation (log (Recruitment) = 9.6- 0.06FSL, $R^2 = 0.14$) between recruitment index in the Shark Bay scallop fishery (northern ground) and Leeuwin Current strength (FSL) between May and August (1983–2006). Dashed line indicates low average FSL conditions where some recruitment was observed to be high. Note 2006 is highlighted as a year with higher recruitment even though FSL was average.

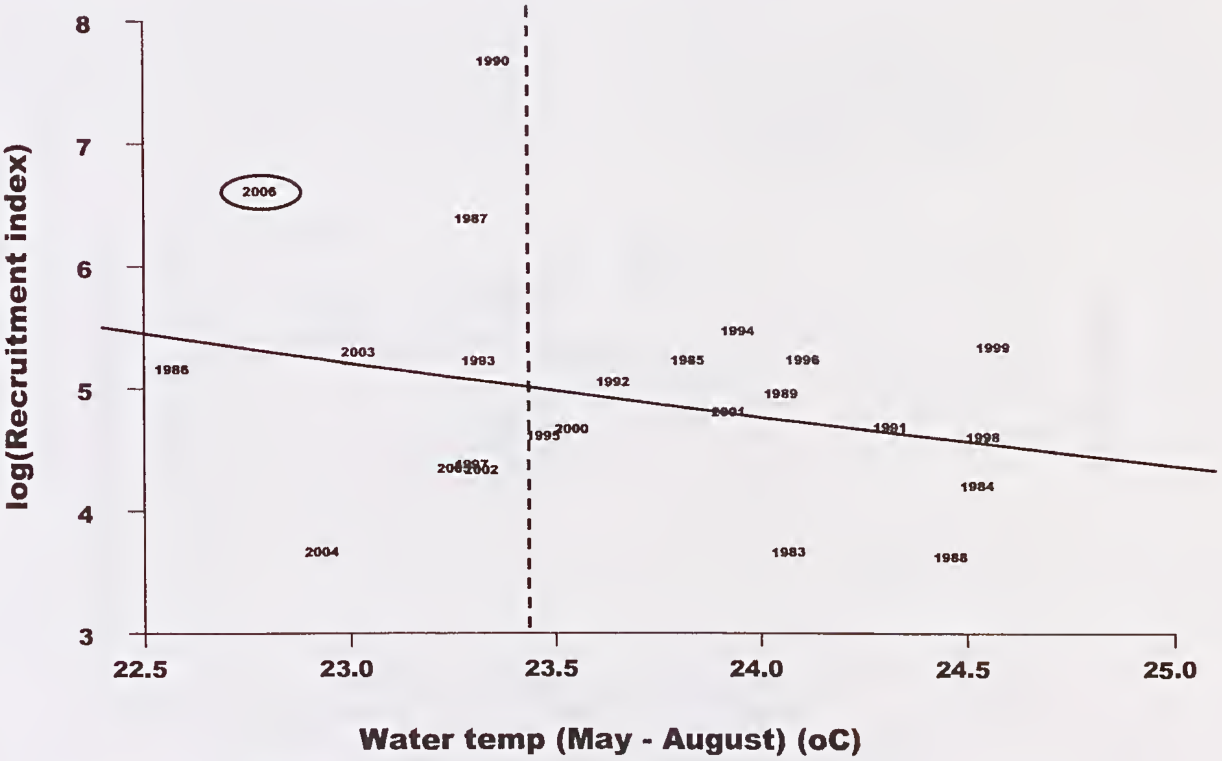

Figure 7. Correlation (log (Recruitment) = 15.8–0.46 SST, $R^2 = 0.08$) between recruitment index in the Shark Bay scallop fishery and surface water temperature (°C) between May and August (1983–2006). The dashed line indicates years when higher recruitment has been observed when Reynolds water temperature in waters of Shark Bay have been less than 23.5°C on average between May and August (when larvae in water column). Also 2006 is highlighted, as high recruitment when LC flow was stronger than for 1987 or 1990.

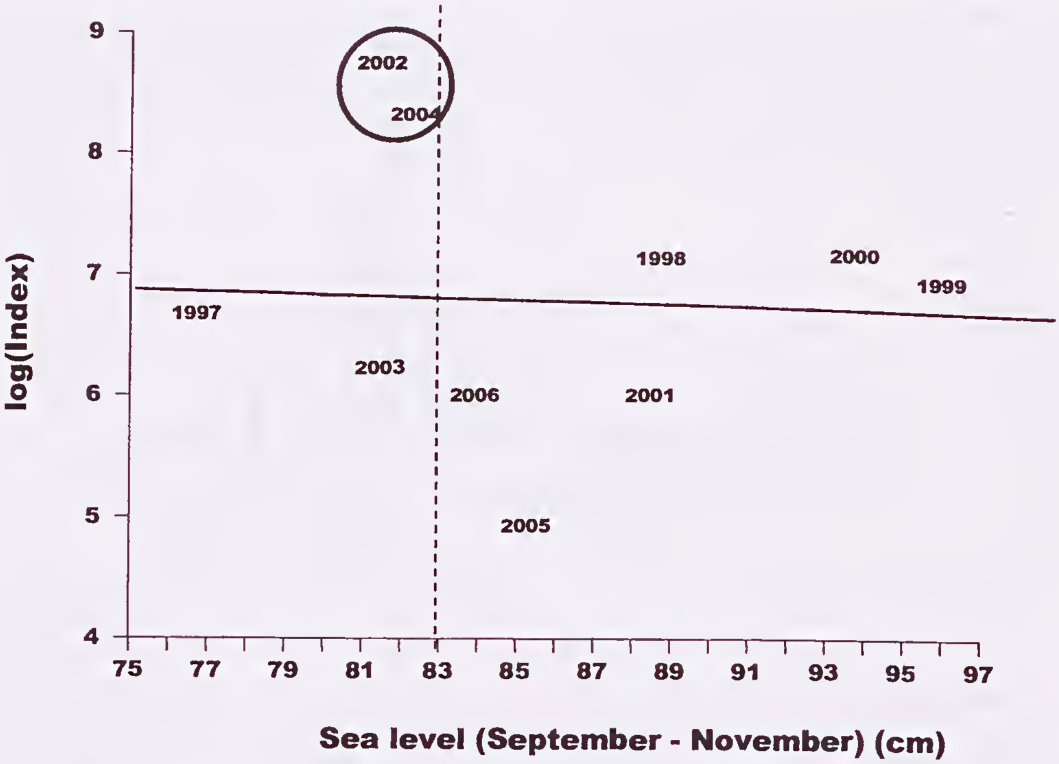

Figure 8. Correlation (log (Index) = 2.02–0.0013FSL, $R^2 = 0.0022$) between recruitment index in the Abrolhos Islands scallop fishery and Leeuwin Current strength (FSL) between September and November (1997–2006). The 2002 and 2004 are highlighted as years of high survey abundances during relatively low FSL resulting in high catches in 2003 and 2005.

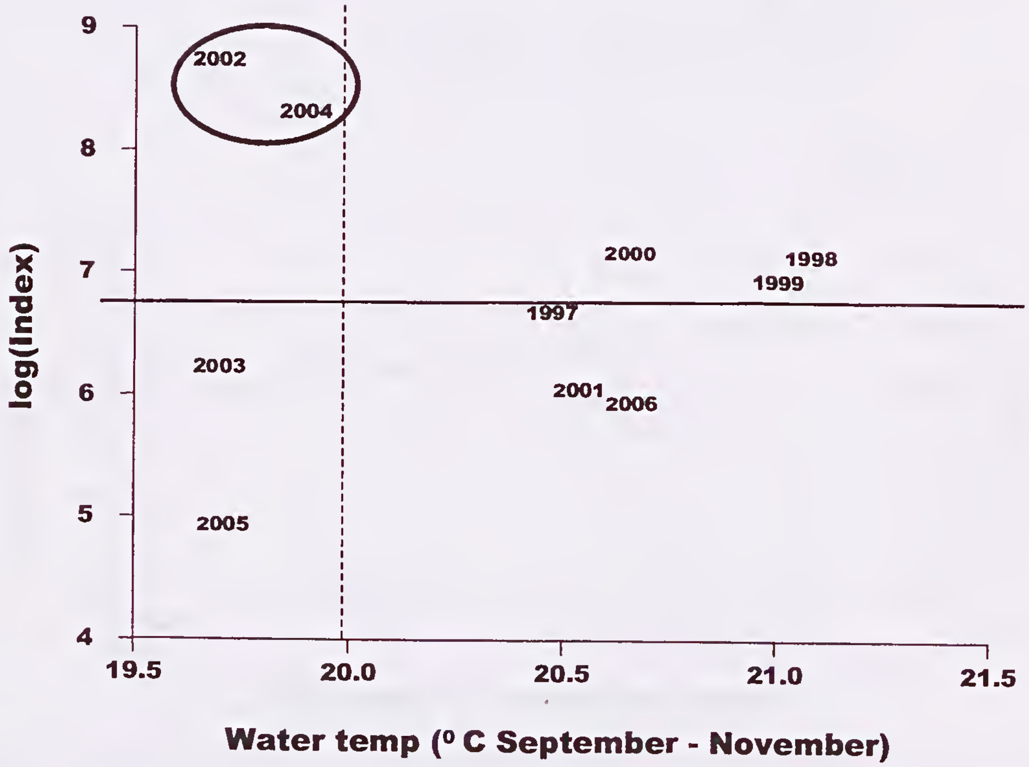

Figure 9. Correlation (log(Index) = 1.89 + 0.0010SST, $R^2 = 1.156E\text{-}5$) between recruitment index in the Abrolhos Islands scallop fishery and Surface Seawater Temperature (SST) between September and November (1997–2006). The 2002 and 2004 are highlighted as years of high survey abundances during relatively low FSL resulting in high catches in 2003 and 2005.

Abrolhos Islands

The high recruitment observed in Shark Bay in 1990 and 1992 (mainly in Denham Sound) resulted in four years of good catches between 1991 and 1994, in particular exceptional catches in 1992 (Joll 1994) (Figure 5a). In the Abrolhos Islands, the peak in catches occurred in 1993 and 1994 (Figure 5b) which would have resulted from good recruitment in 1992 and 1993, indicating a lag of a year or two between these and the high catches in Shark Bay. Standardised surveys were not undertaken in the Abrolhos Islands in the early 1990s so there is no comparative fishery-independent information for this region to indicate when a peak in recruitment may have occurred, although based on current information on lag between recruitment and catch, a good recruitment in 1992 and possibly 1993 is likely. The coincidence of high catches (with a lag) in these two fisheries in the early 1990s were associated with a period of extended ENSO events and subsequent weak LC strength (see Figure 2) and this coincidence has not been observed since. In the Abrolhos Islands, high survey indices were recorded in 2002 and 2004 (Figure 8) (another period of ENSO events and weak LC) and resulted in very high catches in 2003 and 2005 respectively (Figure 5b). There was, however, no carryover abundance in either 2004 or 2006 similar to those observed in Shark Bay in the early 1990s, even though records show that scallops were left on the grounds at the end of each fishing season. This may be due to differences in the timing of spawning resulting in the scallops at the Abrolhos Islands generally being six to twelve months older at the time of harvesting compared to those in Shark Bay.

As was the case for Shark Bay, data from the Abrolhos Islands fishery revealed a relatively poor correlation between the index of recruitment and both the LC strength and water temperature (Figure 9). However again these conditions appear to be pre-requisites for strong recruitment as years of high settlement have occurred under conditions of low LC flow and lower water temperatures (Figures 8 and 9). Another good recruitment occurred in 2007, and was associated with below average FSL and water temperature. These assessments indicate that there are other significant environmental variables that contribute to the success of recruitment besides the strength of the LC and water temperature.

South Coast

The high catch observed in the South Coast Trawl fishery in 2000 (Figure 5c) was in a year of strong LC flow (as was 1999 when recruitment is likely to have occurred), which may have created more optimal conditions (warmer than average South Coast water temperatures) for scallop survival on the south coast. As the scallop larval duration is 2–3 weeks, it is unlikely that larvae could be transported from Shark Bay or the Abrolhos Islands to the south coast over that time period. In fact, the highest catches recorded by fishers during 2000 were from Israelite Bay, the most eastern area of suitable south coast scallop habitat. It is thus extremely unlikely that larvae originating from west coast spawning populations could have been transported that far east. The high catches are more likely to be a consequence of improved environmental conditions on the south coast enhancing survival of larvae produced by the local populations in two successive years.

Shark Bay Western King prawns

Earlier work during the 1980s and 1990s relating western king (*Penaeus latisulcatus*) catches and LC strength showed a very good correlation (R^2 = 0.6, Lenanton *et al.* 1991: R^2 = 0.7; Caputi *et al.* 1996) with higher catches related to stronger LC flows during the March to June period (Figure 10). This was considered to be due to strong LC causing an extension of the peak in

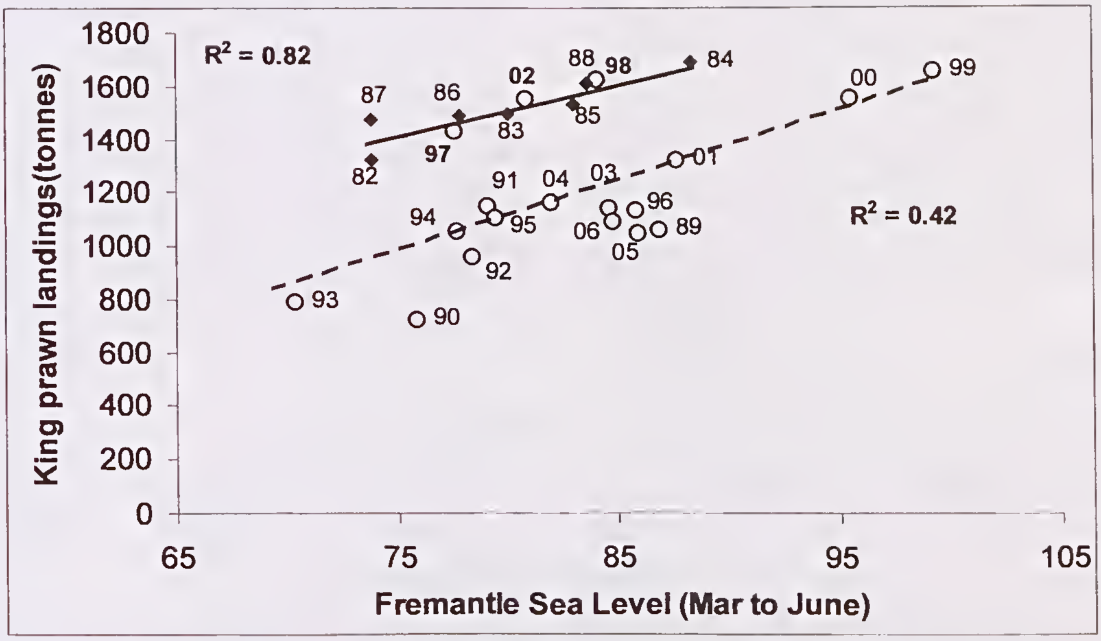

Figure 10. Average Fremantle sea level height between March to June each year and annual western king (*Penaeus latisulcatus*) catches in the Shark Bay prawn fishery between 1982 and 2006. The years highlighted in open circles (from 89 onwards) are included in the dashed line relationship.

the annual temperature cycle to match the main March to June fishing season at a time when king prawns are recruiting onto fishing trawl grounds from the nursery and/or shallow inshore areas. Higher catches were thought to be related to improved catchability, growth and survival (Caputi *et al.* 1996). The updated relationship (Figure 10) reveals that this positive correlation has persisted, but is now much weaker (overall R^2 =0.37). Interestingly, while the relationship is still positive for the years since 1989 (R^2 = 0.42), there has been an overall reduction in total prawn landings (Figure 10). The average landings have reduced from between 1400 and 1600 tonnes annually between 1982 and 1988, to between 1000 and 1200 between 1989 and 2005. The reasons for the lower landings may be related to different targeting and harvesting strategies since the early 1990s, where fishers have tried to save fuel and reduce costs by focusing less effort on larger more valuable prawns as the price of small prawns decreased due to the development of the prawn aquaculture industry.

Mud crabs

In Western Australia, there are numerous examples of the capture of tropical finfish and invertebrates well south of their historical distribution range (Hutchins 1991; Lenanton *et al.* 1991; Hutchins & Pearce 1994). The LC is the mechanism usually invoked as the vector transporting pelagic larvae well south of the normal range of distribution. Exceptionally strong LC during 1999 and 2000 distributed mud crab larvae as far south as Wilson Inlet just west of Albany (Figure 1) on the south coast (Bellchambers 2002; Gopurenko *et al.* 2003). These recruits survived and grew into mature individuals and during subsequent years, were caught by both commercial and recreational fishers. However they appeared not to have successfully bred in the lower west and south coast locations. Thus although they persisted in these more southerly locations for a few years, they did not establish a permanent population. The series of weaker LC since 2000 as a result of ENSO or neutral conditions may not have provided additional recruitment from further north nor the right water temperatures for successful breeding. However, mud crab populations have become established further south of their historical distribution (Shark Bay), perhaps made possible by slight elevations in ambient water temperature as a consequence of warming water temperatures due to "climate change" (Pearce & Feng 2007). One conclusive example is mud crabs having extended its southerly range to include the Murchison, and the Greenough Rivers (Figure 1).

Australian salmon

The western species of Australian salmon is distributed from southwestern WA eastwards to the gulf systems in South Australia (SA). The major part of the breeding stock does not reside along the southwestern coast but undertakes an annual migration from the east in autumn to spawn in this region, with adults then returning to the east. Progeny return to nursery areas in

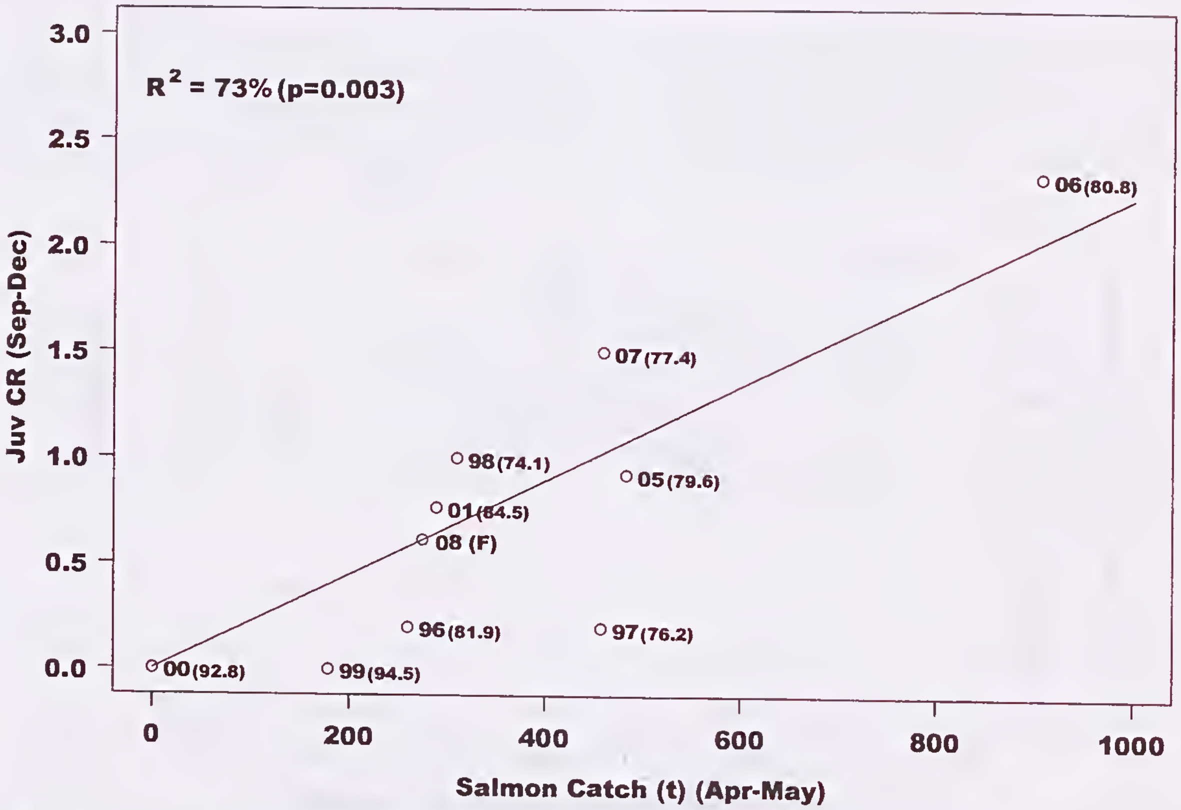

Figure 11. The relationship (Juv CR= - 0.2123 + 2.6414 x 10^{-3} catch (t)) between the annual index of the West Coast Australian Salmon breeding stock (April to May catch), and the annual index of juvenile (0+ yr class) recruitment (measured between September and December of the same year). Mean Fremantle sea level (February to May) is presented in parenthesis after each annual data point. Note that recruitment data were not collected between 2002 and 2004. Recruitment forecast for 2008 is also presented (F).

SA: larvae are thought to be transported east under the influence of the LC (Lenanton *et al.* 1991; Gaughan 2007), and juveniles are assumed to actively swim to nursery areas once able to do so. Historical catch information indicates that relatively few adults and juveniles reside in the south-west region throughout the year.

The strong negative relationships between the south coast commercial log book catch per hour of beach observation [up to 1980s], and LC (Albany sea level in February to April; Lenanton *et al.* 1991) is unable to be updated because a continuing lack of demand for the product and the changing nature of the fishery, has meant the beach-based catches no longer provide a good relative index of adult abundance. However, this is not the case on the lower west coast where a number of fishing teams queue to fish off the same few beaches, where they are afforded seasonal priority of access. Here on the lower west coast, despite reduced demand for the product, the hours of beach observation is believed to have remained relatively constant, and thus catch is still considered to provide a reasonable index of stock abundance. An annual index of recruitment (standardised catch rate of 0+ individuals) of juveniles settling in nursery areas off the lower west coast (the western extremity of the species distribution) (Gaughan *et al.* 2006) is available from research surveys conducted since 1996.

Preliminary analyses have revealed a strong relationship ($R^2 = 0.73$) between the April to May catch (annual index of the breeding stock), and the index of subsequent recruitment to the lower west coast (measured between September and December of the same year) (Figure 11). While the strength of the LC (average monthly FSL between February and May) appears to contribute little to this relationship, the data does reveal that no 0+ yr old recruits were recorded in the West Coast (WC) nursery areas during each of the very strong LC years of 1999 and 2000 (FSL > 92). Elevated indices of recruitment were recorded in both 2006 (2.59) and 2007 (6.91), the most recent (FSL respectively 80.8 and 77.4) of a series of seven weaker LC years experienced off the lower west coast since 2001. FSL was consistently below 85 in all years since 2000. While the breeding stock-recruitment relationship predicts the 2008 recruitment index is likely to be markedly lower than the index measured in 2007 (Figure 11), the extremely strong LC experienced in 2008 (preliminary data indicates that the average monthly FSL between February and May 2008 was 95) is predicted to reduce the level of recruitment even lower. It should also be noted that recruitment surveys were suspended between 2002 and 2004. Thus recruitment indices were not available for those years.

These preliminary results are consistent with those obtained from earlier work conducted at the eastern end of the species range in South Australia, that as expected, shows a strong positive relationship between the index of 0+ recruitment [1979–1989] of juvenile fish into SA nursery areas and the strength of the LC, measured by sea level height in one of the key nursery areas in the SA Gulfs (Lenanton *et al.* 1991). Unfortunately it has not been possible to progress this earlier work, because the juvenile sampling used as a basis for determination of the annual recruitment index in SA has since been discontinued.

Australian herring

Australian herring spawn off the south-west corner of Western Australia between April and May, with a relatively restricted peak in May. Juveniles recruit and settle into coastal and marine embayment habitats along the WA, SA and western Victorian coastlines (Ayvazian *et al.* 2000; Dimmlich *et al.* 2000). Monthly seine netting for 0+ juveniles at numerous locations between Perth and Adelaide was carried out during 1996, 1997 and 1998. These data were used to develop indices of annual recruitment. In order to assess the annual variation in juvenile recruitment, the indices of recruitment were used to model juvenile transport to explain the movement of juveniles from spawning areas to nursery areas. The factors that appear to determine the degree of recruitment success (strength of index of recruitment) are oceanic (the LC) and wind-induced currents and the swimming ability of the juvenile fish. In general, the transport model (Dimmlich *et al.* 2000) indicated that in years of stronger transport, there is a greater recruitment and settlement of juvenile Australian herring east of the Great Australian Bight (GAB) (Figure 1), while in years of weaker current, there was a stronger pulse of juveniles collected from west of the GAB. It seems that the LC was the dominant vector off WA, whilst a wind-driven current dominated off SA. Herring larvae are neustonic. The fact that they experience a single spawning event makes the transported larvae very vulnerable to episodic environment events (such as storms). Also, variable market demand for Australian herring in WA precludes the use of commercial catch and effort data needed to demonstrate links between strong recruitment to SA, and large catch three years later in WA.

Pilchard

Pilchard is the only teleost species from SWA for which there is a reasonable understanding of the dispersal of eggs and larvae. Fletcher *et al.* (1994) showed that winter spawning of pilchard off southern WA resulted in eastward transport of eggs under the influence of the LC, while eggs from summer spawning were transported shorter distances west under the influence of wind-driven surface currents. Gaughan *et al.* (2001) subsequently provided evidence that winter spawned pilchard larvae from the southern WA coast could be transported up to a 1000 km eastwards due to both the LC and seasonally dominant north-westerly winds that generate additional eastward surface drift.

Data was presented (Lenanton *et al.* 1991; Caputi *et al.* 1996) that showed the abundance of 2+ pilchard recruits in the Albany purse-seine fishery was strongly negatively correlated with the strength of the LC (FSL) during the June/July (spawning period) two years earlier [1985–1992]. The potential of considerable eastward transport of pilchard larvae by the LC suggests that such loss of progeny can have a serious impact on recruitment. This relationship deteriorated subsequent to the 1996 review, probably due to other factors becoming more important for pilchard recruitment and thus masking any LC affect. Firstly, pilchard recruitment on the south coast of WA was very low for several years in the mid-1990s, independent of the mass mortality mentioned below.

Secondly, the relationship was affected by a reduction in the overall stock size off Albany as a result of two significant mass mortalities of adult fish, the first in 1995 (Fletcher *et al.* 1997; Hyatt *et al.* 1997) and a second more severe mass event in 1998/99 (Gaughan *et al.* 2000). This has led to dramatic changes in the abundance of mature pilchards and also to their spatial dynamics (Gaughan 2003), relative to the area of influence of the LC.

Whitebait

Annual variation in the catch from a 3-year moving average of catch as an annual index of recruitment variation was positively correlated with LC (FSL) lagged one year [1977–1994] (Gaughan *et al.* 1996; Caputi *et al.* 1996). This promising relationship was updated to include years from 1995 until 2007. Demand for the product has remained strong so annual fluctuations in catch are still considered a good index of abundance, and the residuals (difference between the moving average and the annual catch) still provides a good reflection of the annual variations in recruitment. While there is still a positive relationship between the catch residuals and the FSL during the previous year (Figure 12), the addition of the more recent data weakened the relationship (R^2=0.29), implicating causative factors other than LC.

Dhufish and tailor

Dhufish and tailor are iconic angling species in marine waters off south-western Australia, with the former also a highly valued commercial species. For both species spatial dynamics of their life history are poorly understood. Dhufish spawn in deeper shelf waters while tailor possibly spawn in the vicinity of exposed reefs, usually those some distance off the coast. The larval life history of each is very poorly understood. Similarly, little is known about dhufish juveniles except that they recruit to deep (>10 m) reefs (Hesp & Potter 2000; Hesp *et al.* 2002) whereas juvenile tailor recruit to estuaries and shallow inshore waters where they are frequently caught (Lenanton *et al.* 1996).

Annual indices of recruitment are available for both species. For dhufish, they are derived from the current (2004–2007) age structure, with the numbers in each fully recruited year class back-calculated (taking into consideration mortality and selectivity) to the abundance during the year of initial settlement. Indices have been calculated for each year between 1986 and 2002 (St John unpublished). For tailor, an annual recruitment index has been calculated using data collected from the lower reaches of the Swan River during late summer/autumn months (February to April) that have been shown to be a robust indicator of the abundance of the 0+ and 1+ year classes off the lower west coast of WA (Ayvazian *et al.* in prep.). The abundance of the 0+ year class only has been used in these analyses. These data are available between 1995 and 2008.

Initial comparisons revealed no obvious relationship between LC strength (FSL) and sea surface temperature (SST), and the recruitment indices for dhufish in the waters off the lower west coast of WA. However a strong positive relationship (R^2=0.78) was apparent between recruitment strength, and the average sea surface salinity (measured between November and June, which encompasses the months of spawning and recruitment of

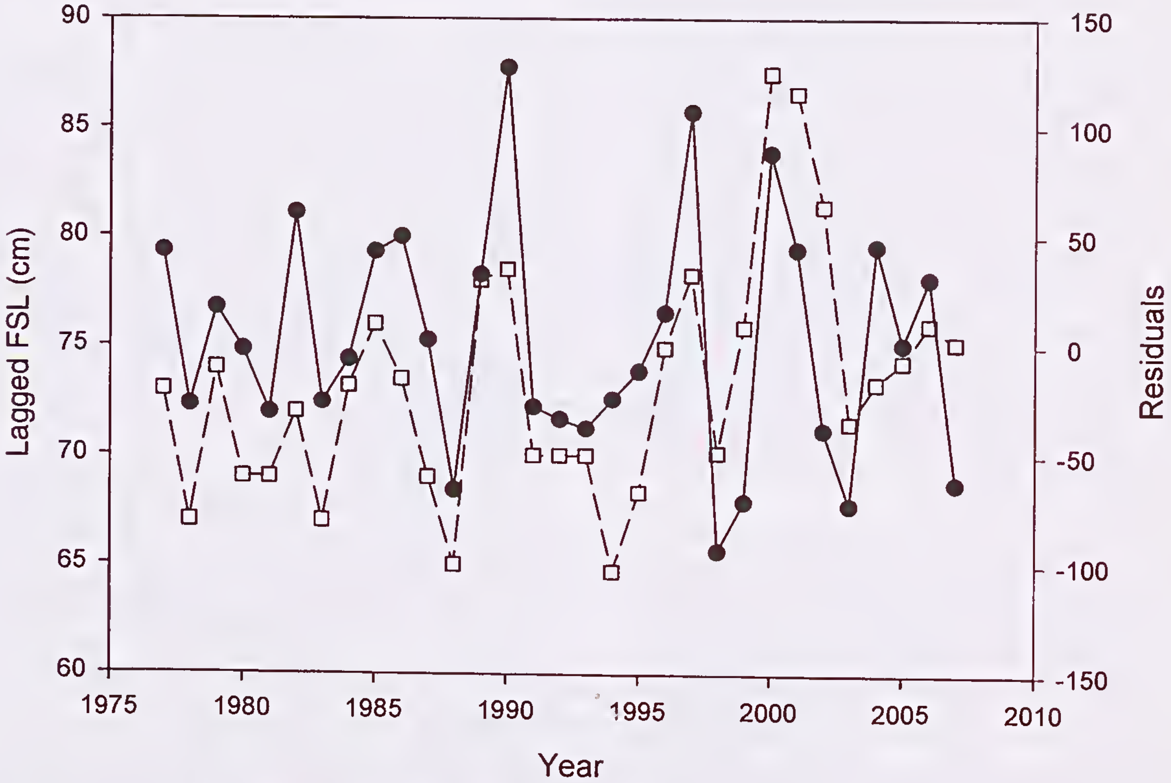

Figure 12. Time series of the residuals of whitebait catches (●), which takes into account the trend in the time series, and sea-level (FSL) time series lagged 1 year (☐).

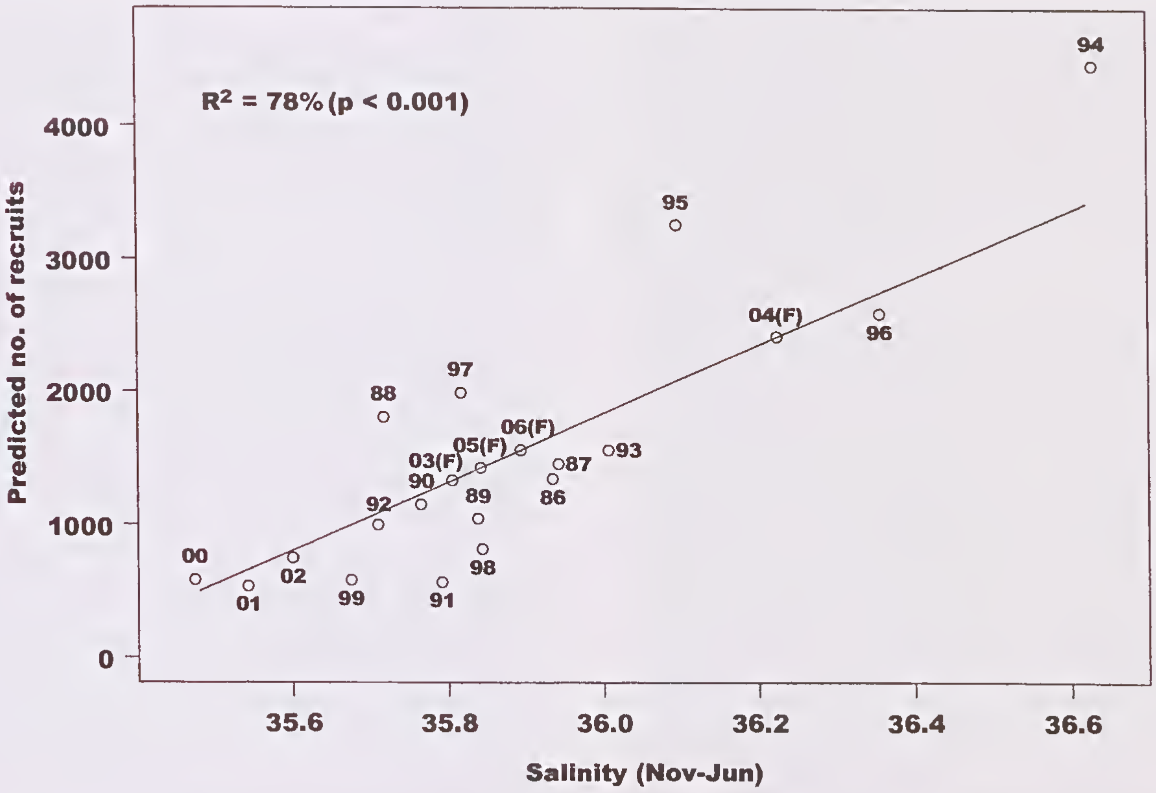

Figure 13. The relationship (Predicted no. of recruits = -82867 + 2348.5 Salinity) between the annual back calculated indices of dhufish recruitment (0+ year class), and the average sea surface salinity (ppt; 35.3‰ = Salinity = 36.7 ‰) of continental shelf waters between Fremantle and Dongara measured between November and May each year. Recruitment forecasts for the years beyond 2002 are shown in parentheses (F).

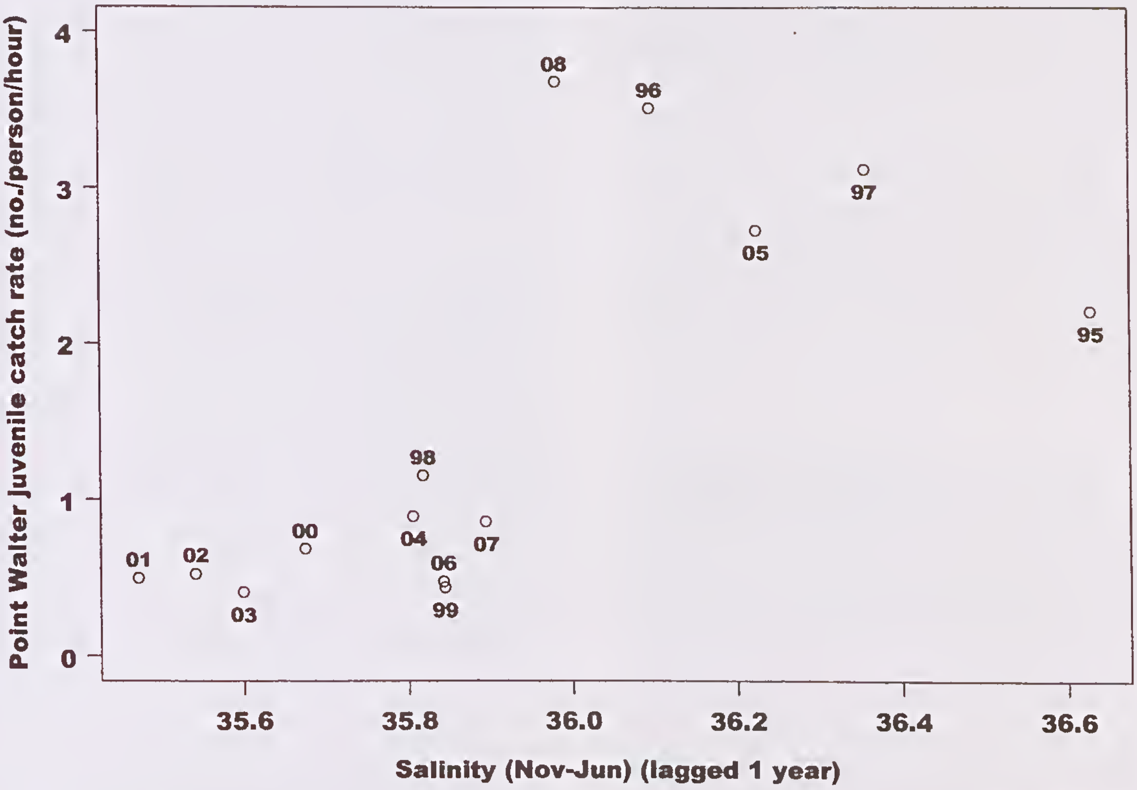

Figure 14. The relationship between the annual index of recruitment of tailor (measured between February and April each year), and the mean salinity of continental shelf waters between Fremantle and Dongara measured between November and May lagged by one year.

this species) of shelf waters between Fremantle and Dongara (Figure 1)(St John unpublished). While more recent recruitment indices for this species are not yet available, the addition of the most recent salinity data (2003 to 2008) suggests that there was one further year of potentially strong recruitment in 2004 (Figure 13).

Interestingly, the key period of spawning and recruitment for tailor is also believed to lie in the period November to June. Initial comparisons between sea surface salinity over those months and the recruitment index, for years between 1995 and 2004, also revealed a strong positive relationship (Ayvazian *et al.* in prep). The addition of more recent recruitment indices data (2005 to 2008, Smith unpublished) has strengthened this relationship (Figure 14). The t-test indicates that mean of the lower (98–04, 06–07)(0.66) and the higher (95–98, 05–08)(3.05) catch rates are significantly different (p-value < 0.001). While these preliminary positive relationships for two quite different teleost species are encouraging, details of the underlying mechanism remains unclear.

However there appears to be two obvious sources of high salinity water encountered on the shelf during summer. One is higher salinity upwelled South Indian Central Water (SICW) (Woo & Pattiaratchi 2008) from areas beyond the shelf, and/or deeper water transported onto the shelf via upwelling from the mixed layer at the base of the LC (Hanson *et al.* 2005; Twomey *et al.* 2007). This latter source of upwelled water is believed to be associated with the Capes Current (Gersbach *et al.* 1999; Pearce & Pattiaratchi 1999). The other is as a consequence of higher rates of evaporation, particularly in inner-shelf regions during years of weak LC (Pearce & Feng 2007; Hanson *et al.* 2005; Waite *et al.* 2007). While evaporation alone is believed to be able to elevate on-shelf salinities, particularly in inshore areas, above 36 ppt (Pearce & Pattiaratchi 1999), it is postulated that the combined effect of upwelling of higher salinity water (up to 35.9 ppt: Gersbach *et al.* 1999; Woo & Pattiaratchi 2008), and the evaporation of this water once on the shelf over the summer months, may together contribute to the salinities >36 ppt (Figures 13 & 14) in offshore shelf waters where dhufish in particular are believed to spawn. The correlation with high salinity may therefore be linked to a physical oceanographic effect, and/or onward effects on the biological oceanography (*e.g.* nutrient status and primary production) that enhances the survival of larvae, and thus recruitment.

General Discussion: Likely mechanisms of the influence of the Leeuwin Current

For some species, such as western rock lobster, the LC relationship appeared robust to the point where the LC strength earlier in the year (Feb–Apr) was used to explain the trend in puerulus settlement later in the same year (peak in Sep–Nov), which was subsequently used to predict the fishery catches three to four years later. The spatial and temporal variability of peak LC flows was also shown to influence catchability of adults of certain species, and thus the magnitude of the commercial catch (Lenanton *et al.* 1991; Caputi *et al.* 1996). On the basis of our current understanding of the behaviour of the LC, and the biology of the species discussed in this paper, WRL appears to be the only species whose larvae genuinely depend on water conditions found at the shelf-break and in the adjacent ocean for their survival (Pearce & Phillips 1988, 1994). It has been postulated that high settlement rates of puerulus into on-shelf nursery areas following their 9 to 11 months of larval life spent off the shelf, may be related to retention within persistent eddies associated with the LC, and favourable physical and biological offshore environment that encourages growth and survival.

The LC behaviour later in the year (Jun–Dec) close to the time of the puerulus settlement also has an advection role in the spatial distribution of the puerulus settlement along the coast. Caputi (2008) has demonstrated that the mean latitude of puerulus settlement is related to the strength of the LC near the time of settlement. Thus WRL could be expected to be the only species of those considered to date that would likely exhibit a sustained and robust relationship with LC strength.

This study highlights the importance of long time series when assessing factors such as environmental conditions affecting recruitment. Relationships based on short times series of data may provide the basis of establishing a hypothesis as to the factors affecting recruitment but confirmation of the relationship can only be established when a longer time series is available. While the LC has a significant effect on the WRL stocks based on a relative long time series of data, it is not the only environmental factor that affects the stock given that it has a long (9–11 mo.) larval phase over a large spatial area. For example, the strength of the westerly winds in winter/spring has also been identified as affecting the puerulus settlement (Caputi *et al.* 2001) and no doubt there are other factors that may be relevant. While these other environmental variables remain within historic ranges, the relationship between the LC and WRL is likely to be maintained. However if we experience environmental conditions outside the historic ranges then it can result in an apparent breakdown in the LC and WRL relationship. The puerulus settlement in 2008/09 may be an example of this as the LC was strong in 2008 and an average or above average settlement would have been expected. However a very low settlement was achieved. An assessment is currently underway as to other factors (biological and/or environmental) that may have contributed to this low settlement.

The reproductive life history stages of most other commercial species appear to be confined to the shelf waters, and are thus to a greater or lesser degree, generally believed to be distributed shoreward of the main area of influence of the LC. Although tongues of LC water can penetrate the shelf for periods of up to several months (Pearce *et al.* 2006), details of the finer-scale shelf behaviour of the LC are still poorly understood. Nevertheless it has been postulated (Gaughan 2007) that under conditions of strong LC flow, large mesoscale eddies can entrain and remove large numbers of pelagic larvae of on-shelf teleost species from the shelf and away from suitable on-shelf nursery areas, thereby contributing to episodes of low annual recruitment, and ultimately contributing to the large annual recruitment variability observed in a number of these teleost stocks. There is however no evidence of an overall negative effect of lobster larvae entrained in these eddies. The very long larval duration of WRL may in fact be an adaptation to cope with entrainment and offshore movement. Depending on its strength at the time when pelagic larvae are present, the LC can also transport larvae considerable distances alongshore from the spawning location (Fletcher *et al.* 1994; Caputi *et al.* 1996), where their ultimate survival will depend on their ability to locate and settle into suitable nursery habitats. For pelagic species whose larvae do not settle to a benthic habitat and that may have a relatively long larval duration, the distance transported can be up to a 1000 km (Gaughan *et al.* 2001), with these advectional processes ultimately being the key determinant of recruitment success (Muhling *et al.* 2008b). Ultimately the effect of alongshore transport by the LC at a whole-of-population level is likely to be different to that at local levels relevant to fishery management boundaries, and the location of fishing grounds. This broad- *versus* local-effect has yet to be considered but would likely differ for species with different larval durations.

Compared to other eastern boundary current coastlines, the coastal waters off SWA have historically been regarded as being characterized by low levels of dissolved nutrients, and as a consequence, were believed to have typically experienced low plankton productivity in the water column (Pearce 1991; Hanson *et al.* 2005; Gaughan 2007). However recent research has shown that nitrate-rich deep water which is located under the LC, can be injected into the euphotic zone and thus generate higher within-water column productivity via upwelling events that extend across the continental shelf. These can occur off the mid-west coast in late autumn and winter (Koslow *et al.* 2008). Localized, but sporadic upwelling events can also be associated with the Capes (Gersbach *et al.* 1999; Twomey *et al.* 2007) and Ningaloo (Hanson *et al.* 2007) Currents during the summer months. Thus it appears that the activity of the Capes and Ningaloo Currents, both of which are components of the LCS, can also influence the composition of the on-shelf larval teleost assemblages (Muhling & Beckley 2007; Muhling *et al.* 2008a), the abundance of individual larval teleosts species, and the levels of recruitment to the fishable stocks of economically important species in coastal waters off SWA. Indeed, ongoing investigations have now revealed that a combination of mean wind speed at Cape Naturaliste and mean salinities measured at four locations along the west coast, and not just salinity (see under Data Sources, and Results and Discussion) during the main spawning period of dhufish were the best available indicators of the activity of the Capes Current, and that these variables were shown to have a positive influence on the annual year class strength of dhufish (Lenanton *et al.* 2009). Similar extensions to the work on tailor are also planned.

As such, the climactic patterns that generate the northern wind stress responsible for generating the Capes and Ningaloo Currents may well be crucial for sustaining stocks of fish in this region.

Summary and Conclusions

Prior to this review, significant correlation between species abundance (juveniles and/or adults) and LC strength could be demonstrated for seven economically important species from water off the west coast of WA. However in all but WRL, and possibly the western king prawn in Shark Bay, the addition of more recent compatible data has either not been possible, or has considerably weakened these relationships. For example, although data have been included from areas outside Shark Bay, all of the LC relationships for scallops are now weaker, indicating that although the LC is still a causative factor, as yet unquantifiable factors appear to also be important.

For a number of the scalefish species, discontinuation of juvenile monitoring (south coast Australian salmon), and changes in the structure and distribution of stocks due to mass mortality (Albany pilchards) have prevented the provision of additional compatible data, and thus precluded the ongoing exploration of these initial relationships. Nevertheless, some interesting additional examples of the influence of the LC have been revealed. LC strength has been identified as an important factor contributing to the transport of Australian herring larvae from WA breeding grounds to nursery areas further to the east off the South Australian coast. Further, a short time series of breeding stock and recruitment indices data from the lower west coast Australian salmon stock have revealed a stock-recruitment relationship where LC appears to have a major "threshold" influence. While no Australian salmon recruitment was recorded along the lower west coast during the two very strong years of LC (1999 and 2000), these unusually strong current events did distribute larvae of a tropical mud crab to lower west and south coast locations well beyond the normal southern distribution of this tropical species.

Two additional interesting relationships (West Australian dhufish and tailor) between juvenile abundance and salinity are also presented. However the underlying mechanisms responsible for these relationships are still in the initial stages of investigation. Because the actual magnitude of salinity change over the period that the relationships cover is very unlikely to exert a physiological effect, it is most likely that salinity is a surrogate for some physical or biological factor *e.g.* increased water column productivity, that enhances survival via increasing growth rate, decreasing mortality and/or increasing ability to access suitable nursery habitat.

From recent research it seems likely that water column productivity is a factor that may enhance the survival of larvae, and thus contribute to the strength of the observed correlations. There is now a better, and still developing, understanding of the sources of variability in pelagic nutrient regimes associated with the waters of the LC in the region of the shelf-break and in adjacent oceanic waters (eddies and meanders), and in nearshore/inner shelf waters (detached macrophyte and terrestrial runoff nutrient sources). However, while there is a broad understanding of the relationships between spatio-temporal variability in nutrient supply and subsequent phytoplankton and zooplankton dynamics, the dynamics of primary production for mid to outer shelf benthic communities in which many of the economically important finfish reside, regrettably, remains poorly understood.

Correlative relationships can continue to provide insight to variability of stock recruitment and fisheries production that is directly relevant to making management decisions. Poor knowledge of the causative agents (single or multiple) may well dictate that fisheries management continues to use plausible hypotheses as an additional source of information for developing scientific advice.

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Pelagic ecology of the Ningaloo region, Western Australia: influence of the Leeuwin Current

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Abstract

The Ningaloo region of Western Australia (WA), best known for its fringing coral reef system, is also an oceanographically unique area that recent studies have revealed as one of the most productive in Australia. Despite the suppression of major upwelling along the WA coast by the poleward-flowing Leeuwin Current (LC), localised seasonal upwelling at Ningaloo is effected by the wind-driven, northward-flowing Ningaloo Current that periodically flows inshore of the LC and enhances nutrient concentrations within the euphotic zone. Under the upwelling-favourable conditions generated during El Niño years, levels of primary production can episodically reach 3000–8000 mg C m^{-2} d^{-1} (as compared to 200 mg C m^{-2} d^{-1} within the bulk of the LC). The diverse copepod fauna of the region is dominated by small, upwelling-ready species that should benefit from these sporadic phytoplankton blooms. However, copepod production rates are generally low (~ 13 mg C m^{-2} d^{-1}) and do not mirror the trends observed with phytoplankton. This disparity is potentially a result of the highly pulsed nature of the upwelling, a strongly advective physical environment and the dominance of microbial processes. It is notable that grazing on picoplankton biomass is extremely high (100%), while the lower (60%) grazing rates on the total phytoplankton community indicate that a substantial portion may be available for export to the benthos. Whale sharks are more abundant at Ningaloo Reef in years in which the Leeuwin Current is strong, but links between the strength of the LC and the seasonal aggregation of other megafauna are weaker. There is also likely significant connectivity between the pelagic production dynamics off Ningaloo and the benthic fauna of the region, although this is currently an under-researched area.

Keywords: Leeuwin Current, Ningaloo Current, Western Australia, primary production, zooplankton, secondary production, megafauna

Introduction

The Ningaloo region of Western Australia (WA), bordering the Cape Range peninsula from about 21°40'S to 23°35'S (Figure 1), is a unique marine environment that supports the most extensive (260 km) western fringing coral reef in the world. The Ningaloo Marine Park was established in 1987 and incorporates most of Ningaloo Reef, in addition to the seabed and overlying waters on the continental slope and shelf to an average distance of 18.5 km offshore. While the region's relatively isolated location has served to limit negative anthropogenic influences as compared to other continental marine parks (Moore 2000), it has also placed some logistical constraints on research efforts. However, over the past two decades or so, oceanographic research programs have increasingly been conducted in the waters off Ningaloo. Here, we review the current state of knowledge on the influence of the Leeuwin Current on the pelagic ecology of the Ningaloo region, including nutrient fluxes, pelagic primary productivity, zooplankton dynamics, and the characteristic marine megafauna of the region.

Physical oceanographic setting

The large-scale oceanographic dynamics off Ningaloo can be characterised by two main scenarios, depending on season. Whilst the poleward-flowing Leeuwin Current is present year-round (Figure 2), the flow rate and volume transport is largest between April and September (Godfrey & Ridgway 1985). The presence of an extensive coral reef at Ningaloo is closely linked with the LC, as this warm, downwelling current serves to increase ambient temperatures as compared to similar latitudes off the west coasts of South America and Africa, particularly during winter (Pearce 1991; Morton 2003). Physical connectivity between the Leeuwin Current and reef waters is particularly facilitated towards the

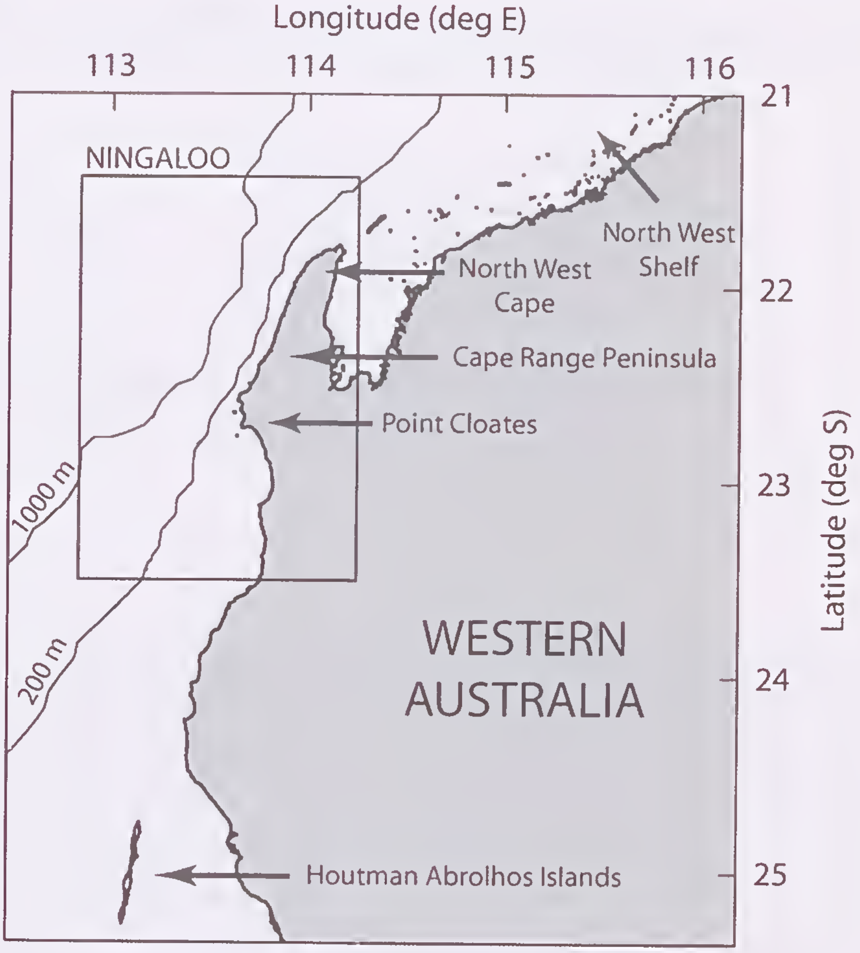

Figure 1. Location of the Ningaloo region of Western Australia.

northern extent of the Ningaloo region, where the continental shelf is the narrowest in Australia (6–10 km).

During summer, strong southerly winds generate a northward current, the Ningaloo Current (NC), on the continental shelf between the LC and the reef front (Figure 2b). The NC generally predominates on the shelf from September to April, forming a wide (30 km) flow on the broad shelf off Point Cloates (Figure 1) that rapidly tapers to 2 km or less as it flows northward along the narrow shelf (Taylor & Pearce 1999). Recent field and modelling data has indicated that a significant proportion of the NC volume is sourced from LC surface waters, via a persistent re-circulation feature at Point Cloates (Figure 2; Woo *et al.* 2006a,b). A contribution to the Ningaloo Current's volume is also sourced from upwelling of deeper (~ 100 m) and colder water from the base of the LC, below the upper mixed layer depth (Hanson *et al.* 2005; Woo *et al.* 2006). However this relatively small-scale upwelling can be fairly cryptic in nature, as the strength of the Ekman transport is not always sufficient to advect the colder water through to the surface where it could be detected by satellite imagery (Hanson *et al.* 2005; Woo *et al.* 2006a; Furnas 2007).

On an interannual basis, the strength and volume of the LC are closely linked to the El Niño/Southern Oscillation (ENSO) cycle. The interannual ENSO signals are transmitted from the Pacific across the Indonesian Throughflow, and travel along the WA coastline as coastally trapped waves (Meyers 1996; Wijffels & Meyers 2003). High coastal sea levels correspond to stronger LC flow during La Niña years, and contrast with low sea levels and weaker flow during El Niño years (Pearce & Phillips 1988; Feng *et al.* 2003, 2004). The latter scenario allows for increased seasonal upwelling activity off northwestern Australia (Wilson *et al.* 2003a; Condie & Dunn 2006; Furnas 2007).

Pelagic ecology off Ningaloo

The Leeuwin Current, Ningaloo Current and primary production

The oligotrophic Leeuwin Current is typified by very low dissolved nutrient levels (generally < 0.2 μM nitrate, < 0.2 μM phosphate) within the upper mixed layer, with a nutricline present between 100 and 200 m depth (Pearce *et al.* 1992; Hanson *et al.* 2005). Accordingly, primary productivity rates within the LC and adjacent oceanic waters can be quite low, measured at a mean of 200 mg C m^{-2} d^{-1} north of the 28°S during the summer (Hanson *et al.* 2005). Though recent field work has shown that the presence of the downwelling LC does not completely suppress Ekman-type upwelling off northwestern Australia (Woo *et al.* 2006a,b), the oligotrophic nature of the LC does place limits on the nutrient levels that are transported into the euphotic zone by the adjacent NC upwelling. During a study in the summer of 2000,

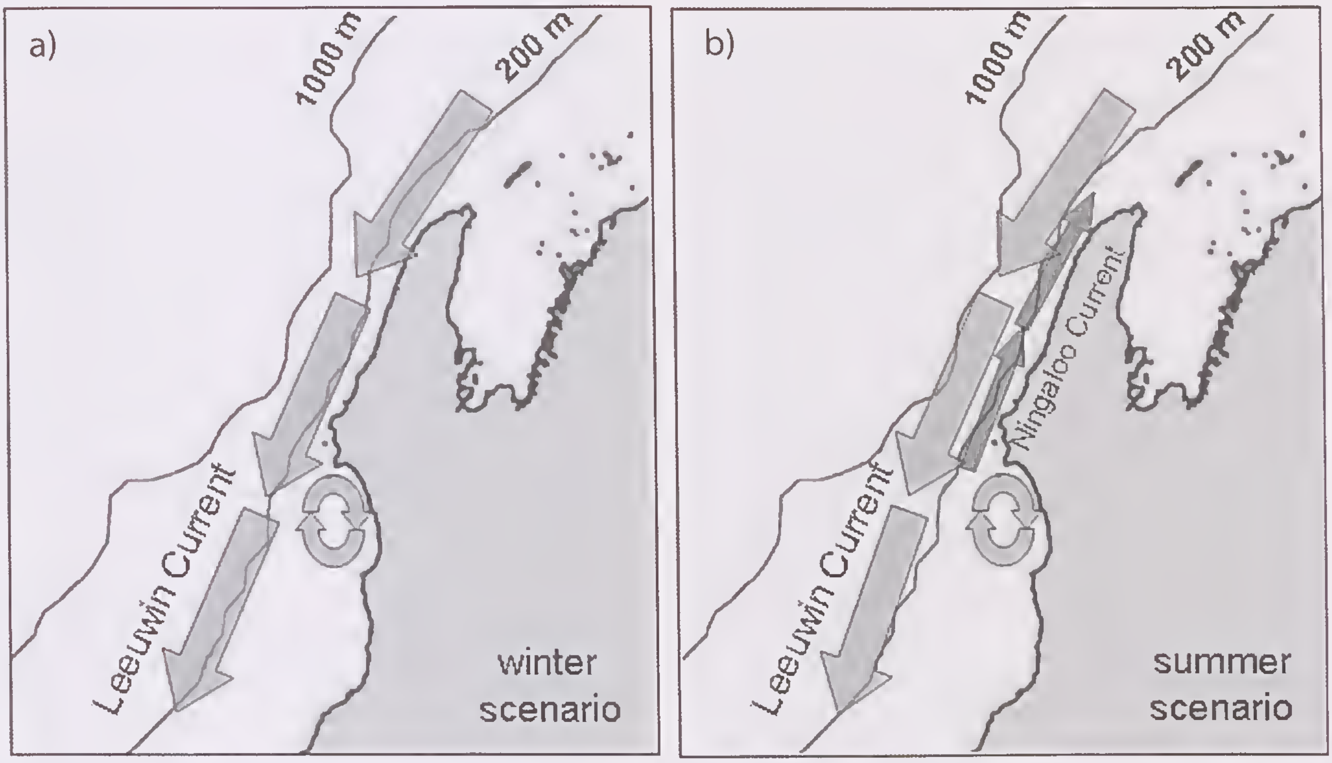

Figure 2. Generalised seasonal circulation patterns off the Ningaloo region, indicating a) the dominance of the Leeuwin Current along the shelf break during the winter months and b) the presence of the northward-flowing Ningaloo Current during the summer months. The re-circulation pattern south of Point Cloates is a persistent feature.

maximum nitrate concentrations were ~ 2–6 mM in upwelled water within the euphotic zone (~100 m) off North West Cape (Hanson *et al.* 2005), substantially lower than in the major upwelling regions associated with equatorward eastern boundary currents (*e.g.*, up to 20–30 mM NO_3^- in the eastern Pacific; Dickson & Wheeler 1995; Kudela *et al.* 1997).

The relatively modest level of nutrient enrichment (~ 2–6 mM nitrate) resulting from upwelling generates primary production rates off Ningaloo that are significantly higher than in the LC proper. Total water column productivity off the Cape Range peninsula ranged between 850 and 1300 mg C m^{-2} d^{-1} (Hanson *et al.* 2005), and have been measured as high as 3000–8000 mg C m^{-2} d^{-1} off North West Cape (Furnas 2007), though these high rates were not sustained. These high rates of primary productivity undoubtedly play an important role in the food web dynamics of the region. For example, it is unlikely to be a coincidence that the highly productive Ningaloo Current is located next to a major coral reef system and adjacent to the rich prawn fishery in Exmouth Gulf, the second largest in WA (770–1500 tonnes yr^{-1}; Kangas *et al.* 2006).

The original view of phytoplankton communities within the LC, primarily obtained via ocean colour satellite imagery (Pearce *et al.* 2000), was one of extremely low biomass (0.1 mg chl *a* m^{-3}). However, recent *in situ* measurements found significant vertical biomass gradients, with phytoplankton forming a deep chlorophyll maximum (DCM) associated with the nitracline at the base of the LC's mixed layer (Hanson *et al.* 2005, 2007a). These DCMs (which are also maxima of phytoplankton carbon) can have chlorophyll concentrations of 0.9 mg m^{-3} or higher, and in the LC are associated with a maximum of 30 to 70% of total water column production. However off the Ningaloo region, the upwelling dynamics and shoaled nutricline can result in a DCM layer that is relatively shallow (~ 30–40 m depth; Hanson *et al.* 2007). The large phytoplankton populations in these layers are able to take advantage of higher light levels at these depths, resulting in an extremely productive DCM that can account for 80–95% of total water column production and yet remains largely beyond the range of surface-based satellite biomass measurements.

During the summer of 2000, phytoplankton community composition within the Leeuwin Current and offshore waters showed only 40–55 % similarity to Ningaloo Current waters (based on HPLC pigment analysis), displaying high proportions of picoplankton such as cyanobacteria in surface waters and prochlorophytes at the DCM (Hanson *et al.* 2007b). In contrast, diatoms and haptophytes were found to be more prevalent in the Ningaloo Current. The size-fractionated work by Furnas (2007) showed that large phytoplankton > 10 mm (particularly centric diatoms) were common off NW Cape during upwelling conditions. These species are classically associated with nutrient-rich conditions with significant 'new' inputs of nitrate, leading to the relatively short and productive 'herbivorous' food chain from large phytoplankton to copepods to fish (Cushing 1989). Yet interestingly, Hanson *et al.* (2007b) found that ammonium-driven 'regenerated' production (which is typically based on recycling of nitrogenous nutrients within the food web) can dominate throughout the study region, accounting for over 80% of total nitrogen uptake even in the upwelling-influenced Ningaloo Current. Nitrogen recycling via the multi-layered microbial food web (which leads from bacteria and picoplankton to protozoa, ciliates and microzooplankton; Azam *et al.* 1983; Cushing 1989) has been shown to complement the shorter nitrate-based herbivorous food chain within upwelling zones (Codispoti 1983; Probyn *et al.* 1990; Bode *et al.* 2004), and in the Ningaloo region seems to play a large part in sustaining productivity levels that may have initially been generated by advective nitrate fluxes.

The biological impact of upwelling in the Ningaloo region is a function of: (a) conditions within the Leeuwin Current (*e.g.*, depth of mixed layer and nutricline), (b) the strength and duration of upwelling-favourable winds (*i.e.*, the intensity of upwelling), and (c) geographical location, primarily with respect to the width of the continental shelf and resultant proximity of upwelling flows to deep nutrient pools (Hanson *et al.* 2005). Furnas (2007) compared the effect of different physical forcing scenarios occurring El Niño and La Niña years on phytoplankton and bacterial dynamics. During El Niño years, the Leeuwin Current is weaker, with a thinner mixed layer and a higher associated frequency of coastal upwelling events (Condie & Dunn 2006; Furnas 2007). During upwelling events in the El Niño summer of 1997/98, there were episodes of very high primary production – up to 8000 mg C m^{-2} d^{-1} (as measured by the incorporation of ^{14}C-bicarbonate). These production events were strongly pulsed – measurements at the same slope station a few days apart differed by over a factor of four (Furnas 2007) and did not generally persist. However, during the La Niña of 1998/99 a stronger Leeuwin Current suppressed the tendency of the system to upwell, and resulted in generally lower rates of primary production, and fewer instances of production exceeding 2000 mg C m^{-2} d^{-1}.

Measurements of oxygen flux in the water column indicate that the waters immediately adjacent to Ningaloo Reef are strongly autotrophic, with P:R ratios between 2 and 6 (Table 1). Respiration rates frequently exceed 1000 mg C m^{-2} d^{-1}, possibly reflecting bacterial degradation of detrital material within the water column, and net primary productivity rates using the oxygen flux method frequently exceed 2000 mg C m^{-2} d^{-1}. Bacterial production rates on the slope off North West Cape, measured from the incorporation of ^{3}H-thymidine, were correlated with primary productivity rates (~18% of primary production), and were on average 6-fold higher in El Niño conditions than in La Niña conditions (median 620 mg m^{-2} d^{-1}, cf 110 mg m^{-2} d^{-1}; Furnas 2007).

The intensity of coastal upwelling (most prevalent during El Niño years) is also closely linked to the ambient wind field (Barber & Smith 1981), further highlighting the episodic nature of any associated nutrient fluxes. The large phytoplankton biomass and high productivity measured off Ningaloo may provide a seasonally predictable, but patchily distributed, input of food resources to the micro- and mesozooplankton populations within the region (discussed below), which in turn are regularly exploited by the large filter feeders (*e.g.*, manta rays and whale sharks) that are seasonal visitors to this region (Taylor 1994). The extent of such bottom-up control of trophic structure off Ningaloo is certainly one area requiring further research.

Zooplankton dynamics

There is no data available on the zooplankton communities of the Leeuwin Current per se, though studies are in progress (Strzelecki *pers. com.*). Further south (31°), off Perth, the microzooplankton (Paterson *et al.* 2007) and mesozooplankton (Strzelecki *et al.* 2007) communities of warm core rings largely originating from the LC have been described. Microzooplankton abundance in the vicinity of North West Cape was 620 cells L^{-1} (Moritz *et al.* 2006), but 1500–2600 cells L^{-1} in the warm core eddy off Perth (Paterson *et al.* 2007). Tranter (1977a) and co-workers described copepod, euphausiid, amphipod and euthecostome communities in the eastern Indian Ocean along the 110° E meridian between 9° and 32° S, and taken together with the study of Strzelecki *et al.* (2007) the data straddle the area of influence of the LC but do not include it. Moreover, differences in sampling methodology (plankton net mesh size and sampling strategy) make direct comparisons between mesozooplankton studies difficult.

Copepods are the dominant organisms in the mesozooplankton of the Ningaloo area (McKinnon & Duggan 2001), and >120 species were recorded from stations occupied around North West Cape. Small calanoid copepods belonging to the families Paracalanidae and Clausocalanidae dominate, together with small cyclopoid copepods belonging to the Oithonidae, Corycaeidae and Oncaeidae (McKinnon *et al.* 2008). The dominant genera of small calanoid copepods (*e.g.*, *Calocalanus*, *Paracalanus*, *Clausocalanus*) are common

Table 1

Community respiration (CR) and net primary production (NPP) at Ningaloo Reef in April of 2003 and 2004. The P:R ratio represents the ratio of gross primary production (CR+NPP):CR. See McKinnon *et al.* (2007) for methods.

Date	Latitude	Longitude	Depth (m)	CR	NPP	P:R
				(mg C m^{-2} d^{-1})		
11-Apr-02	21 35.95	113 59.68	250	550.29	561.28	2.02
16-Apr-02	22 41.03	113 32.93	100	1735.71	2680.39	2.54
19-Apr-02	22 43.35	113 36.35	52	1250.91	2260.16	2.81
24-Apr-03	22 43.88	113 38.30	28	597.02	1647.35	3.76
26-Apr-03	22 44.27	113 36.78	56	1045.14	2503.35	3.40
28-Apr-03	22 45.14	113 32.96	70	1171.29	5517.64	5.71
29-Apr-03	22 43.10	113 36.27	50	579.96	2142.32	4.69

generalist suspension feeders that are pre-adapted to upwelling, in that they are able to achieve life cycle closure under these advective conditions (Peterson 1998). The most notable absence from the Ningaloo fauna is *Calanoides carinatus*, a copepod that is characteristic of upwelling regimes, despite its occurrence in the broader region (Tranter 1977b). It therefore appears that upwelling is too infrequent and episodic to sustain a zooplankton fauna specific to upwelling regimes.

Generally, the action of the Leeuwin Current entrains a southward flow of water off the shallow NW shelf. McKinnon *et al.* (2003) documented the effect of Cyclone Tiffany on the plankton communities of the NW shelf. This cyclone moved in a SW direction, pushing the water and plankton ahead of it down to the vicinity of NW Cape, causing an elevation in water temperature, and a shift in plankton communities toward those typical of the inshore tropical environments to the north. The movement of the Leeuwin Current probably has the same effect, by entraining shallow water tropical coastal communities southward – as indicated by the contribution of small, typically inshore calanoid copepods such as *Bestiolina similis* and *Parvocalanus crassirostris* to the copepod communities in the vicinity of Ningaloo.

Macrozooplankton, as sampled by light traps, were more abundant in El Niño conditions than in La Niña conditions, primarily because of the greater contribution of amphipods (Wilson *et al.* 2003a). Subsequent macrozooplankton research in the vicinity has focused on krill (Euphausiacea), as these were believed to be important resources targeted by megafauna (see below). The most abundant euphausiid in the area is *Pseudeuphausia latifrons* (98% of euphausiid catches), though 3 other species do occur (Wilson *et al.* 2003b). *P. latifrons* was more abundant in La Niña conditions, possibly because of a preference for warmer water (Wilson *et al.* 2003b).

Unfortunately, despite the obvious abundance of gelatinous zooplankton in the area, there is no published information.

Bongo net collections made in the vicinity of NW Cape contained the larvae of 76 families of fishes (Sampey *et al.* 2004). In the two summers of that study, there was a similar community composition in each year, though some families (*e.g.*, Pomacentridae, Carangidae) showed differences in abundance. Most larvae preyed upon copepods, and individual families of fishes exhibited strong selection for particular taxa (Sampey *et al.* 2007). Late stage larvae sampled with light traps were threefold higher in La Niña conditions, and differed markedly in community composition between El Niño and La Niña years (Meekan *et al.* 2006a), and richest catches occurred at stations characterised by high mixing.

Secondary production and food chains

Dilution experiments conducted near NW Cape indicate that ~100% of picoplankton (*Synechococcus* and *Prochlorococcus*; counted by flow cytometry) production is grazed each day, but only ~60% of the total phytoplankton community (as indicated by chlorophyll a concentration) is grazed by micrograzers (McKinnon *et al.* unpublished); these estimates are consistent with those of Paterson *et al.* (2007, 2008), further south. This implies that the balance of primary production is consumed within the water column by meso- and macrozooplankton or settles out to become available to benthic consumers. One of the unresolved challenges in the ecology of the NW is to account for the carbon source which drives benthic food chains in the area. Exmouth Gulf, in particular, has a very productive prawn fishery; in the absence of significant terrigenous inputs the only source of primary production that could drive this fishery is pelagic.

In spite of the differences observed by Furnas (2007) in primary production rates near NW Cape between El Niño (weak LC) and La Niña years, copepod production rates measured on the same cruises did not differ substantially (McKinnon & Duggan 2001, 2003), and were generally low (~13 mg C m^{-2} d^{-1}). We suspect the cause of the anomaly between high rates of primary production and low rates of secondary production is the highly pulsed nature of upwelling, a strongly advective physical environment and a domination of food web structure by microbial processes. The dominance of microbial processes hinted at from the results of the dilution experiments can be confirmed by a comparison of primary and secondary production rates (Table 2). Copepods are highly inefficient grazers of particles <2μm in size; therefore restricting the primary production numbers to the range of cell sizes available to copepod grazers and comparing that to their production rates, we find that the food web linking primary production to mesozooplankton is only ~1% efficient. Similar calculations on upwelling systems, such as the Benguela, result in trophic efficiencies of the order of 10%.

Low rates of secondary (copepod) production off the coast of NW Australia are reflected further up the food chain by fisheries statistics. Catches of finfish species off the Western Australian coast are low by world standards (Lenanton *et al.* 1991), and the large biomass of pelagic planktivores characteristic of other eastern boundary current ecosystems does not occur. Meekan *et al.* (2003) compared the growth rates of the coral reef fish *Pomacentrus coelestis* in El Niño (upwelling favourable, high plankton production) and La Niña years (lower incidence of upwelling, lower plankton production, higher water temperatures). Fish grew faster in the La Niña year, suggesting that in this case, temperature rather than food supply was more important in determining growth rate.

Table 2

Pelagic food chain efficiency. Primary production is taken from the data of Furnas (2007), and copepod production from McKinnon & Duggan (2003), meaned over 10 field trips in two summers (Oct–Feb).

		Shelf	Shelf Break
>2μm primary production	mg C m^{-3} d^{-1}	38	13
Copepod production	mg C m^{-3} d^{-1}	0.4	0.1
Transfer efficiency	%	1.2	1.1

The Leeuwin Current and the movement of megafauna

The seasonal aggregation of whalesharks at Ningaloo Reef between March and June of each year is one of the best known features of the area, and is the basis of a lucrative ecotourism industry. The cause of this predictable occurrence is still open to speculation, but the most likely explanation is a trophic one. Taylor (1994) proposed that whale sharks fed on aggregations of zooplankton and small fish associated with the coral spawning that occurs at this time of year. However, such short-lived events do not explain the occurrence of whale sharks in the area for a period of months. Whale sharks are known to feed on aggregations of chaetognaths (Rowat *et al* 2008), plankton (Taylor 1996), tropical krill (Wilson & Newbound 2001; Jarman & Wilson 2004), fish spawn (Heyman *et al.* 2001) and baitfishes (Wilson *et al.* 2006). At present there is nothing known about the annual patterns in abundance or behaviour of plankton and their predators in waters adjacent to Ningaloo, in part because of the logistic difficulty of sampling in offshore waters year-round. However, the occurrence of episodically high plankton production and the seasonal aggregation of large planktivores in the same geographic area is a co-incidence too large to ignore.

The Leeuwin Current is strongest between April and September (Godfrey & Ridgeway 1985). There is currently no data to indicate where whale sharks arriving at Ningaloo have come from, but it is known that many sharks return to the area each year (Meekan *et al.* 2006b; Bradshaw *et al.* 2007). Whale shark abundance at Ningaloo is negatively correlated to the SOI, indicating that there are more sharks in years in which there is a strong LC (Sleeman *et al.* in press). In this case, it may be that the sharks "ride" the Leeuwin Current to arrive at Ningaloo (as suggested by Wilson *et al.* 2001). Tagging studies of whale sharks indicate that the animals move in a northerly direction, toward Indonesia, when they leave Ningaloo Reef, in which case they would be swimming against the LC and possibly using it as a directional cue (Wilson *et al.* 2006) . Archival tagging studies (Wilson *et al.* 2006) indicate whale sharks are easily capable of diving to considerable depth, and could avoid the influence of the current by diving beneath it. Despite this, the depth records shown by Wilson *et al.* (2006) are predominantly shallow.

Other megafauna occur in waters adjacent to Ningaloo Reef, including humpback and pygmy blue whales, dolphins, sharks, turtles, manta rays and dugongs. However, biophysical variables, including those such as SST that may be correlated with the influence of the Leeuwin Current, accounted for only a small proportion of the variance in abundance of megafauna (Sleeman *et al.* 2007).

Links to the benthos

To date, investigations into the coupling between pelagic and benthic dynamics at Ningaloo have been limited. The physical effect of the Leeuwin Current on dispersal of benthic (and also pelagic) organisms is two-fold. Firstly, the net movement of propagules is southward with the dominant current flow, and is responsible for the occurrence of tropical animals in SW Australia (Hutchins 1991 and papers therein). Secondly, the formation of the NC forms a closed cell in which local propagules may well be retained, and coral spawning within the Ningaloo region may be timed to coincide with the presence of the NC (Taylor & Pearce 1999). Simpson (1991) examined the mass spawning of scleractinian corals along the WA coast, which generally coincides with periods of maximum seawater temperatures (March/April at Ningaloo) and the annual intensification of the Leeuwin Current, which would provide a physical mechanism for the southward dispersal of coral planulae. As also suggested by Babcock *et al.* (1994), this would potentially result in unidirectional (southward) gene flow between WA coral reefs (*e.g.*, from Ningaloo to reefs at the Abrolhos Islands; Figure 1). However, recent genetic studies by Whitaker (2004, 2006) on three species of broadcast spawning corals at Ningaloo found restricted genetic mixing even at distances of 7–24 km, suggesting that large-scale dispersal from the Ningaloo region may be relatively infrequent.

There is likely to be significant connectivity between the pelagic production dynamics off Ningaloo and the benthic fauna of the region, although there is little published work on this theme. In 2004, a series of deep water (to 200 m depth) biodiversity surveys off Ningaloo revealed significant populations of benthic filter feeding organisms, particularly sponges and gorgonian corals (Rees *et al.* 2004). It is interesting to speculate on the potential links between the nutrition of these filter feeders, the productive deep chlorophyll maximum layers within the Leeuwin and Ningaloo Currents, and seasonal influxes of live and detrital particulate material associated with summer upwelling blooms. In shallower waters, there is significant exchange between shelf waters and those of the reef lagoon, with wave action transporting shelf water over the reef front and lagoon waters escaping to the shelf through the reef gaps (Taylor & Pearce 1999). Studies currently underway aim to quantify the fraction of reef productivity driven by oceanic nutrient sources at Ningaloo, using biomarker techniques and coral laboratory studies (A. Wyatt, *pers. comm.*).

Conclusions

The Leeuwin Current is the primary physical forcing factor determining the pelagic ecology of the Ningaloo region off Western Australia, with the key dynamics highlighted in this paper illustrated schematically in Figure 3. Series of episodic, cryptic upwelling events have been observed during the summer months off Ningaloo, especially during El Niño years when the Leeuwin Current is weaker and the wind-driven Ningaloo Current is stronger. Under these conditions, Ekman transport results in moderate influxes of nutrients within the euphotic zone that can generate localised events of high phytoplankton productivity. Based on grazing rates and levels of mesozooplankton production, it is apparent that microbial-scale processes may be key to the pelagic trophodynamics of the region (Figure 3). There are many unresolved challenges in understanding the ecology of the waters off Ningaloo, including determining annual patterns in both primary and secondary production, and quantifying the links between pelagic and benthic dynamics.

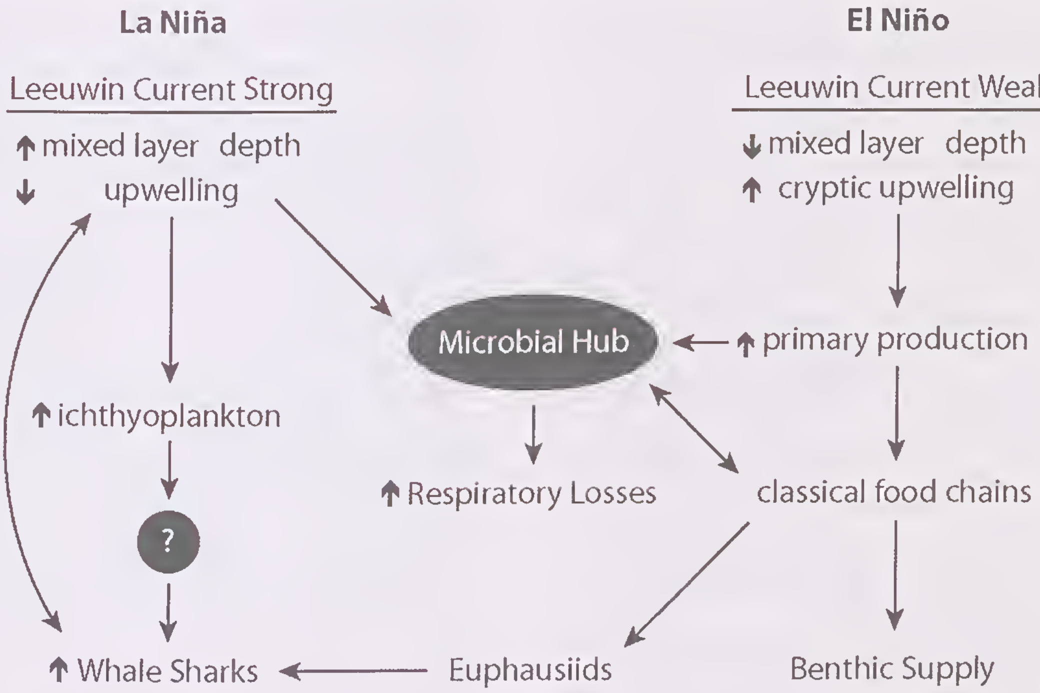

Figure 3. Schematic indicating the key linkages within the pelagic ecology of the Ningaloo region, and the impact of the contrasting physical forcing scenarios under La Niña and El Niño conditions.

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Influence of the Leeuwin Current on the Marine Flora of the Houtman Abrolhos

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Abstract

The influence of the Leeuwin Current on the marine flora of the Houtman Abrolhos is examined. The marine plants (seaweeds and seagrasses) are assessed by comparisons of the Houtman Abrolhos species diversity and composition relative to a nearby coastal region (Jurien Bay), using the tropical and temperate floras of Western Australia as benchmarks. Our results demonstrate that, in terms of assemblage structure and taxonomic distinctness, the marine flora of the Houtman Abrolhos clearly represent a transitional zone between tropical and temperate regions, with the strong tropical influence a direct result of the Leeuwin Current. In contrast, the nearby inshore flora of the Jurien Bay region exhibits a much lower, almost negligible tropical influence.

Introduction

The Houtman Abrolhos is an archipelago of 122 mainly coral islands lying some 65–90 km offshore from Geraldton, Western Australia, at a latitude of 28 to 29°S. They include the southernmost examples of major coral reefs in the eastern Indian Ocean and are one of the highest latitude reef systems in the world (Wells 1997). The islands sit near the northern limit of what is known as the 'western overlap zone', a broad region extending from Cape Leeuwin in the south to North West Cape in the north. The flora and fauna of this region shows, to varying degrees, the southern temperate influence as well as the northern tropical.

It is well documented that the marine biota of the Houtman Abrolhos includes a high proportion of tropical species that would generally not be found at such high latitudes. These species would appear to owe their presence to the influence of the Leeuwin current, which brings warm waters from the tropics along the coast of Western Australia (Maxwell & Cresswell 1981; Morgan & Wells 1991; Huisman 1997; Pearce 1997; Wells 1997). This hypothesis, however, has never been tested in any meaningful or statistically robust way and doing so is the motivation behind the present contribution.

The influence of the Leeuwin Current can be sporadic, and this juxtaposition of warm tropical water with the colder water more typical of these latitudes encourages unusual associations and contributes to a wide diversity of organisms (Hatcher 1991; Huisman 1997). It is one of the few places where temperate kelps such as *Ecklonia radiata* (C.Agardh) J.Agardh can be seen growing intermixed with tropical corals. It is thought that the warmer and nutrient-poor waters of the current promote coral growth at the expense of macroalgae, but periodic upwelling of nutrient-rich water promotes extensive algal growth (Hatcher 1991). Hatcher (1991) drew parallels between the Houtman Abrolhos and the Galapagos, another archipelago where 'coral and macroalgal communities vie for dominance' the outcome dependent on local oceanography.

Marine Plants

Until relatively recently, the marine flora of the islands was poorly known. Only sporadic records appear in the literature (*e.g.*, Lucas 1926; May 1946, 1951; Levring 1953), mostly derived from collections made by the 'Percy Sladen Trust' expeditions of 1913 and 1915 (see Dakin 1918–1922) or collections made by school groups (Sammy 1972) and presently lodged in the Adelaide herbarium. These publications included, at most, only a few species (Huisman 1997). The same description could also be applied to much of the Western Australian coastline, with, until recently, the level of knowledge of the flora severely limited northward of Perth and becoming even more so into the tropics (Huisman *et al.* 1998). Recently, however, there has been a marked increase in activity. During the early 1990s one of us (JH) visited the Houtman Abrolhos on numerous occasions to collect marine plant specimens. Several new taxa were described as a result (*e.g.*, Huisman & Gordon-Mills 1994; Huisman & Kraft 1992, 1994; Huisman & Millar 1996) all of which were included in a catalogue for the islands by Huisman (1997). The flora of the tropical Dampier Archipelago was documented by Huisman & Borowitzka (2003) and Huisman (2004). Underwater photographs of many

Western Australian species were included in Huisman (2000) and Huisman *et al.* (2006). These publications represent only a small section of ongoing floristic and taxonomic studies of the Western Australian marine flora by JH and JP. In addition, collections held on the Western Australian Herbarium (PERTH) have recently been databased and the information made available via the Department of Conservation and Environment's 'FloraBase' website http://florabase.dec.wa.gov.au/). The PERTH collection now includes all marine plant specimens previously held by CSIRO, Murdoch University, and the University of Western Australia and therefore includes the vast majority of important historical and contemporary collections. As well as collection data for each specimen, also included in the PERTH database are precise location coordinates.

In addition, the 'Australian Marine Algal Name Index' is now available through the Commonwealth Department of Environment and Water Resources website (http://www.anbg.gov.au/abrs/online-resources/amani/). This index collates all published records of algal species in Australia and can be searched in a variety of ways, including by State boundaries, broad bioregional provinces (*e.g.*, the tropical Dampierian Province or the temperate Flindersian Province) or, in a few instances, by more precise localities (*e.g.*, the Houtman Abrolhos).

Added to this trove of information are the significant records generated by surveys undertaken by one of us (JP) and jointly identified (JP and JH). These surveys include the Jurien Bay region, allowing us an onshore focus with which comparisons with the Houtman Abrolhos can be drawn.

Thus the level of knowledge since the previous Leeuwin Current Symposium in 1991 has increased manyfold and the scope for analyses of species' distributions and regional biodiversity has been greatly expanded. Given this wealth of new resources, we have undertaken analyses in an attempt to:

1. Assess, in a statistically meaningful way, the biogeographical affinities (tropical versus temperate) of the Houtman Abrolhos marine flora, and:
2. Compare the flora with that of Jurien Bay region, the nearest onshore locality that we have comparable data for.

The Environment of the Houtman Abrolhos Islands

The Houtman Abrolhos archipelago sits some distance offshore on the edge of the continental shelf and is subjected to a different set of environmental parameters relative to nearshore localities such as Geraldton and Jurien Bay. The most significant difference is the influence of the Leeuwin Current, as the archipelago lies in the direct path of the current and often receives its full force, whereas the nearshore experiences very little direct influence. This was first noted by Saville-Kent (1897), who recorded the waters surrounding the islands to be approximately 2°C warmer than those inshore and suggested that this was due to a southward flowing current sitting offshore. The impact of the Leeuwin Current on the Houtman Abrolhos environment has subsequently been documented by several authors (see Pearce 1997). While it appears that the Leeuwin Current is the dominating environmental feature, other factors should not be excluded.

Winds

Winds at the Houtman Abrolhos and nearshore were reviewed by Pearce (1997) and Chua (2002), and a detailed analysis of hourly and seasonal Houtman Abrolhos winds for 1995 was included in Sukumaran (1997). Generally there are strong seasonal southerlies (*i.e.*, northward) during late autumn to early spring, whereas the winter winds are much more variable due to gales and also periods of calm (Steedman & Associates 1977). The seasonal wind pattern is similar at both the Houtman Abrolhos and the mainland coast (Pearce 1997), but the wind strength tends to be greater at the Abrolhos (Abrolhos: mean wind speed in winter 6.5 m/s and summer 8.6 m/s; Geraldton airport: 4.4 m/s winter and 6.9 m/s summer) (Pearce 1997).

There is a diurnal seabreeze wind cycle evident both at the Houtman Abrolhos and the coast, although the pattern is somewhat weaker offshore (Pearce 1977). The seabreeze patterns and wind speeds are stronger during summer months than in winter. At Jurien Bay, easterlies (blowing offshore) dominate in the mornings, with the seabreeze coming in at 10 to 15 m/s from the south/southwest/west in the afternoon (Chua 2002). At the Abrolhos, these diurnal patterns were less marked, but there is a southeasterly wind in the morning followed by a southwesterly in the afternoon (Sukumaran 1997).

Currents

The Leeuwin Current is the dominant ocean current off the Western Australian coast, flowing southwards along the edge of continental shelf and therefore directly affecting the Houtman Abrolhos islands (Pearce 1997). Satellite images show a variety of current jets and meandering waters off the archipelago, ranging from southward currents (the Leeuwin Current) brushing the islands to large offshore anticlockwise eddies causing (potentially) northward currents along the shelf break (Pearce 1997). Records from current-measuring moorings for the period September 1986 to August 1987 were reported by Boland *et al.* (1988). These showed the southward Leeuwin Current flowing at up to 50 cm/s (1 knot) offshore of the Abrolhos, with the strongest and most persistently southward flow in November 1986 and between February and June 1987, and more variable directions (and lower speeds) in January and June/July (see also Pearce 1997). Satellite buoy tracks (*e.g.*, Pearce 1997) also indicated onshore flow through the Islands and into the nearshore waters on occasion.

Currents on the continental shelf were very much weaker and also more variable in direction (with more current reversals) (Pearce 1997; Boland *et al.* 1998). This variability was also observed by Cresswell *et al.* (1989), using earlier current meter data from the mid-1970s. Generally there was a southward flow between March and August 1974 (p.117) and northward at other times of the year. Pulses of onshore/offshore currents with speeds generally <20 cm/s have been recorded (Pearce 1997), but there is little direct influence of the Leeuwin Current near the coast.

Chua (2002) deployed a current meter in Essex Lagoon (near Jurien) for 2 weeks in August 2002 (*i.e.*, winter) to validate his modelled currents. This recorded a predominantly southward flow at speeds of up to 15 cm/s, highly correlated with the wind although also influenced by other factors (p.60–62).

Water temperature

The only long-term time-series data at the Houtman Abrolhos (Rat Island) and inshore (Dongara, Jurien) are from Fisheries Western Australia temperature loggers recording hourly. Pearce *et al.* (1999) reported monthly mean temperatures at Rat Island ranging from 19.5°C (August) to 23.3°C (March), Dongara ranging from 17.5°C (July) to 23.9°C (February), and Jurien ranging from 18.3°C (September) to 22.2°C (March), based on data from 1990 to 1994. The temperature data reported by Pearce (1997) and Pearce *et al.* (1999) clearly shows that the Leeuwin Current maintains warmer temperatures at the Houtman Abrolhos over winter, effectively dampening atmospheric influences and restricting the annual variation to approximately 20–24°C, a range of 4°C. In contrast, the shallow coastal waters of Dongara are more directly influenced by atmospheric conditions, warming to 24°C in February and dropping to less than 18°C in July/August, an annual range of 6°C and in phase with coastal air temperatures.

Salinity

Water samples taken monthly at the same sites as the temperature loggers (Pearce 1997) showed salinity ranges at Rat Is. of 35.37 (July) to 35.74 (January); Dongara 35.40 (July) to 36.34 (February). The higher inshore salinities in summer are due to evaporation, whereas the lower offshore salinities in winter are due to the Leeuwin Current.

Tides

Observed tides at the Houtman Abrolhos and inshore are mainly diurnal with a small amplitude of 0.5 to 1 m (Pearce 1997), with a high correlation between the two areas (Pearce 1997). Water movement due to wind and atmospheric pressure changes can have a marked impact, and as a result predictive tide tables can be unreliable. Tidal currents are negligible because of the small tidal range (Chua 2002)

Materials and Methods

Species data

Our marine plant data are derived from species lists generated by several surveys conducted in each region. Houtman Abrolhos data were predominantly collected by JH during qualitative surveys conducted during the 1990s (Huisman 1997). Records for the Jurien Bay region (here defined as the area extending from Wedge Island (30°49'43"S, 115°11'18"E) to Dongara (29°15'17"S, 114°55'05"E) consist largely of the extensive collections made by JP during 2003 to 2006 as part of CSIRO's quantitative ecological surveys of the region (Babcock *et al.* 2006) and joint CSIRO/Western Australian Museum surveys conducted in March 2006. All marine plants were hand-collected from five randomly placed 0.25 m^2 quadrats at 45 sites located throughout the region, covering both reef and seagrass habitats at varying depths and levels of wave exposure. All specimens were identified to species level by either JP or JH. Species data from these surveys were supplemented by additional records of lodged specimens from other collectors held in the Western Australian Herbarium (PERTH). Quantitative data were converted to presence-absence data prior to analyses.

Benchmark floras from the Dampierian and Flindersian Provinces were extracted from the 'Australian Marine Algal Name Index' (http://www.anbg.gov.au/abrs/online-resources/amani/), representing tropical and temperate floras of Western Australia, respectively, and were included in analyses. The biogeographic provinces follow the scheme illustrated by Womersley (1981) and later (with slight modifications) by Huisman (2007; p. 544, Fig. 77), who note that the distribution of marine algae appears to agree with most of these provinces. Species data for these provinces were extracted from the database of specimens lodged at the Western Australian Herbarium (PERTH).

Data analyses

Multivariate analyses were performed in PRIMER v6 (Clarke & Gorley 2006) following transformation of all data to presence/absence species lists for each region. A non-metric multi-dimensional ordination (nMDS) was then performed, using a Jaccard similarity measure. Additionally, the average taxonomic distinctness (Δ^+) was calculated, which is an intuitive measure of biodiversity that measures the average degree to which species in each region are related to each other (Clarke & Warwick 1998; Warwick & Clarke 1998; Ellingsen *et al.* 2005). Taxonomic distinctness analysis was used because it is independent of sampling effort and not influenced by the number of observed species (Clarke & Warwick 1998). Taxonomic distinctness incorporates the number of species present as well as the path length linking each pair of species in a hierarchical classification (see Clarke & Warwick 2001 for full equation).

In this study the taxomonic levels used for marine plants were species, genus, family, order and division, according to the classification described by Guiry & Guiry (2008). Equal path lengths were used between taxonomic levels to calculate Δ^+, such that the path length for different species in the same genus was 20, while species that were related only at the highest taxonomic level (*i.e.*, belonging to the same division) had a path length of 100. Following computation of Δ^+, values were tested for the departure of Δ^+ for each region from the overall value of Δ^+ expected for the 'global' species list, from 1000 independent simulations for each subset size (no. of species, m = 200, 250, 300, … 800) drawn randomly from the 'global' total of 987 algal species.

Results

A total of 295 and 341 species were recorded from the Houtman Abrolhos and Jurien Bay region, respectively.

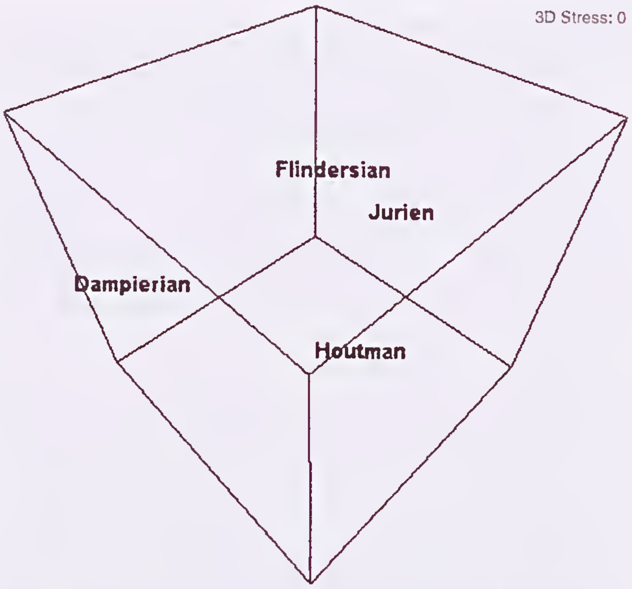


Figure 1. Non-metric 3-dimensional scaling plot of algal regions used in this study, based on presence/absence species data for each region.

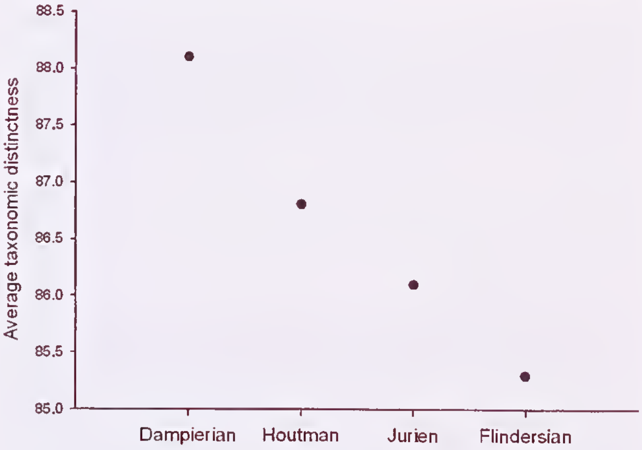


Figure 2. Average taxonomic distinctness for each of the four algal regions, arranged from north to south (L to R). $R^2 = 0.98$.

Of these, 13.6% of species recorded from the Houtman Abrolhos were endemic to the area (when compared with other areas included in this study), compared with 2.6% for the Jurien Bay region. Furthermore, 9% of Houtman Abrolhos marine plants have a tropical affinity (Table 1) compared with only 0.9% of species from the Jurien Bay region. Using the Dampierian flora as a benchmark for the tropical flora of Western Australia, it was found that 25% of species were common to the Houtman Abrolhos and tropical Dampierian Province. A similar proportion of species were common to both the Houtman Abrolhos and the temperate Flindersian Province. Markedly different trends were seen in the Jurien Bay region flora; around 17% of species were shared with the Dampierian flora, compared to 39% shared with the Flindersian flora.

The ordination based on the assemblage-level data showed a large separation (*i.e.*, high dissimilarity) between the floras of most regions (Figure 1). The least similarity observed among regions was between the

Table 1

Tropical algal species recorded from the Houtman Abrolhos (information updated from Huisman 1997)

RHODOPHYTA

Amphiroa fragilissima (Linnaeus) Lamouroux
Antithamnion antillanum Børgesen
Botryocladia skottsbergii (Børgesen) Levring
Callophycus serratus (Harvey ex Kützing) Silva
Ceramium macilentum J.Agardh (as *C. mazatlanense* Dawson)
Ceratodictyon spongiosum Zanardini (Figure 4H)
Chondria dangeardii Dawson
Chrysymenia kaernbachii Grunow
Chrysymenia ornata (J. Agardh) Kylin
Coelothrix irregularis (Harvey) Børgesen
Corallophila huysmansii (Weber-van Bosse) Norris
Dasya iyengarii Børgesen
Dasya pilosa (Weber-van Bosse) Millar
Endosiphonia spinuligera Zanardini
Parviphycus tenuissimus (Feldmann & Hamel) Santelices (as *Gelidiella pannosa* Feldmann & Hamel)
Gelidiopsis variabilis (J. Agardh) Schmitz
Gloiocladia indica Weber-van Bosse
Gloiocladia rubrispora (Searles) Norris
Gracilaria canaliculata Sonder
Lomentaria corallicola Børgesen
Monosporus indicus Børgesen
Platysiphonia victoriae (Harvey ex J.Agardh) Womersley & Shepley (as *Platysiphonia corymbosa* (J.Agardh) Womersley & Shepley)
Platysiphonia marginalis Wynne, Kraft & Millar
Polysiphonia gracilis Tseng
Predaea laciniosa Kraft
Predaea weldii Kraft & Abbott
Spirocladia barodensis Børgesen
Titanophora pikeana (Dickie) Feldmann (as *T. weberae* Børgesen) (Figure 4E)
Trichogloea requienii (Montagne) Kützing (Figure 4B)
Yamadaella caenomyce (Decaisne) Abbott

CHLOROPHYTA

Anadyomene plicata C. Agardh (as *A. brownii* (Gray) J.Agardh) (Figure 4F)
Boodlea composita (Harvey) Brand
Caulerpa fergusonii Murray
Caulerpa mexicana Sonder ex Kützing
Caulerpa racemosa var. *corynephora* (Montagne) Weber-van Bosse
Caulerpa racemosa var. *lamourouxii* (Turner) Weber-van Bosse
Caulerpa racemosa var. *peltata* (Lamouroux) Eubank
Caulerpa racemosa var. *turbinata* (J. Agardh) Eubank
Caulerpa serrulata (Forsskål) J. Agardh
Caulerpa webbiana Montagne
Codium geppiorum Schmidt (Figure 4G)
Dictyosphaeria cavernosa (Forsskål) Børgesen (Figure 4C)

PHAEOPHYCEAE

Dictyota ceylanica Kützing
Dictyota mertensii (Martius) Kützing
Padina boryana Thivy (as *Padina tenuis* Bory de Saint-Vincent)

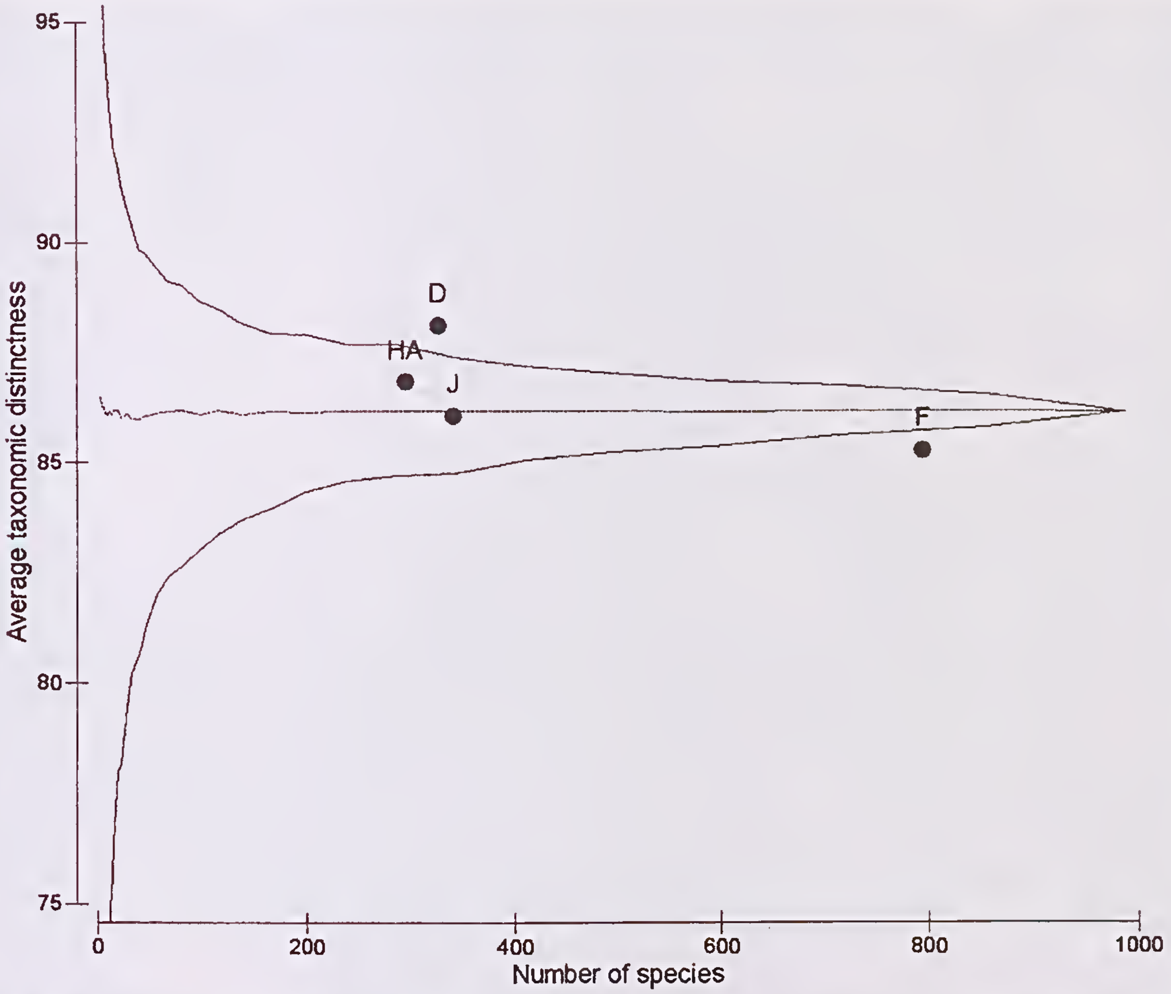


Figure 3. The 95% probability limits (solid upper and lower lines of 'funnel') for the average taxonomic distinctness of algae (Δ^+) from 1000 simulations for a range of species subset sizes. Also shown are the actual values for each algal region plotted against the number of species recorded in each region, and the Δ^+ for the 'global' list of 987 algal species (dashed line). D = Dampierian; F = Flindersian; HA = Houtman Abrolhos; J = Jurien.

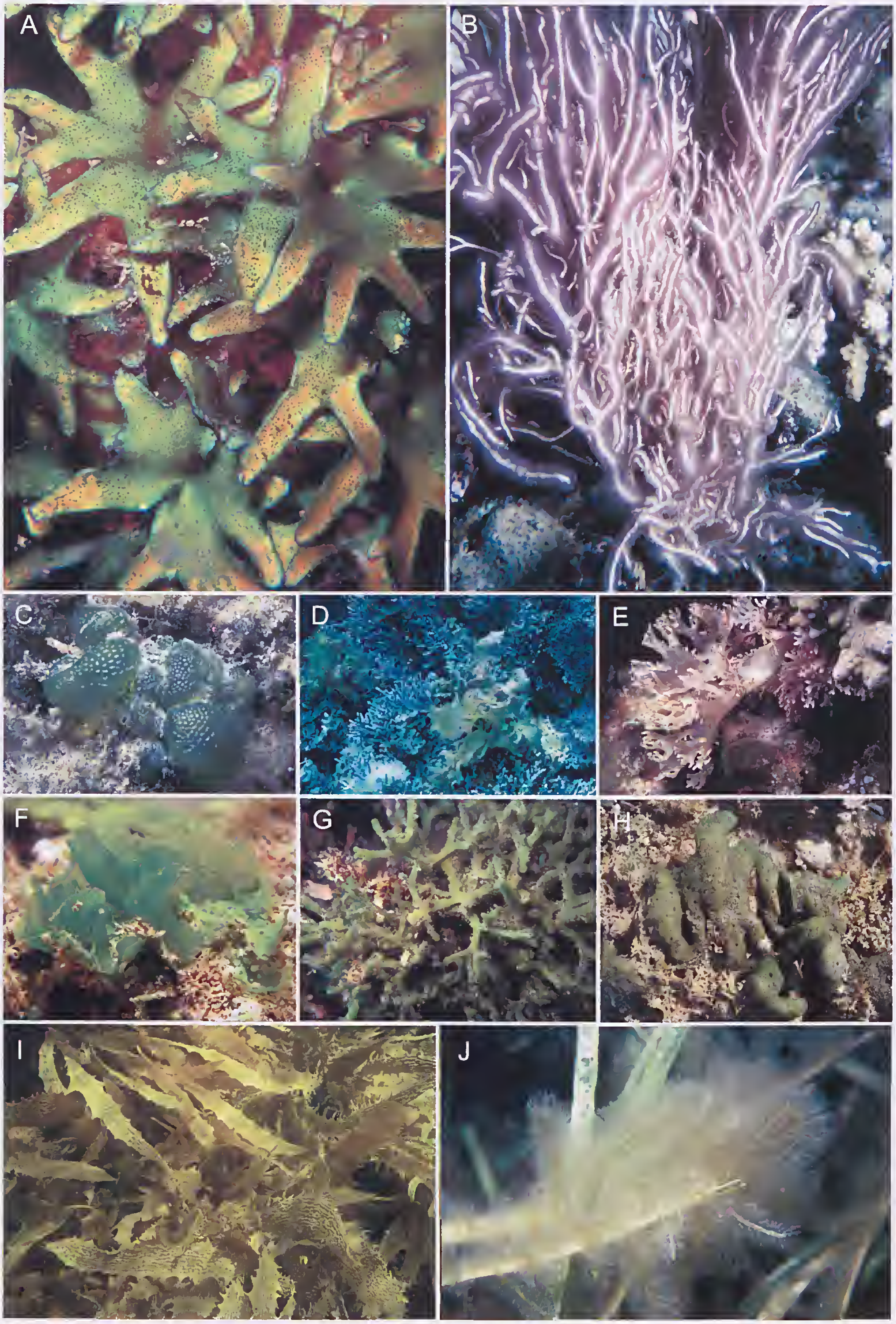
Jurien Bay region and the tropical Dampierian assemblage (Jaccard similarity = 17.6%), while greatest similarity (39.1%) was between the Jurien Bay region and the temperate Flindersian assemblage. When considering the similarity between the Houtman Abrolhos assemblage and those of other regions, it showed a similarity of 25.2% and 32.8%, respectively, to the Dampierian Province and Jurien Bay region.

The average taxonomic distinctness (Δ^+) decreased with increasing latitude south (Figure 2), indicating greater taxonomic breadth, or biodiversity, in regions closer to the tropics. The temperate Flindersian flora had the lowest taxonomic biodiversity of all regions considered.

Testing for the departure of calculated values of Δ^+ from expected values based on the 'global' master list revealed that the 'benchmark' temperate Flindersian flora, despite having the greatest number of species recorded (S = 794), had significantly lower than expected Δ^+ ($p = 0.002$; Figure 3). Conversely, the Δ^+ of the 'benchmark' tropical Dampierian flora was significantly greater than expected ($p = 0.002$). The floras of the Houtman Abrolhos and Jurien Bay regions fell within the expected range (95% CI) of Δ^+ values.

Discussion

The marine flora of the Houtman Abrolhos islands is a diverse assemblage, and as previously noted (Huisman 1997) includes a mixture of species from both tropical and temperate origins. The former category includes typically tropical taxa such as the green algae *Boodlea composita* (Harvey) Brand, *Caulerpa webbiana* Montagne, *C. cupressoides* (West) C. Agardh, *C. lentillifera* J. Agardh, and the red algae *Asteromenia exanimans* Saunders, Lane, Schneider & Kraft (Figure 4A), *Trichogloea requienii* (Montagne) Kützing (Figure 4B), *Spirocladia barodensis* Børgesen, *Predaea weldii* Kraft & Abbott, *Titanophora pikeana* (Dickie) Feldmann (Figure 4E), and *Ceratodictyon spongiosum* Zanardini (Figure 4H) (see Table 1). Examples of taxa with more temperate affinities are the green algae *Caulerpa obscura* Sonder, *C. simpliciuscula* (R. Brown ex Turner) C. Agardh, *Codium laminarioides* Harvey, the brown algae *Myriodesma quercifolium* (Bory de Saint-Vincent) J. Agardh, *Asperococcus bullosus* Lamouroux (Figure 4J), *Ecklonia radiata* (C.Agardh) J.Agardh (Figure 4D, 4I) , and the red algae *Carpothamnion gunnianum* (Harvey) Kützing and *Hennedya crispa* Harvey. Many of these species are at the southernmost limit (in the case of tropical species) or northernmost limit (in the case of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temperate species) of their distribution at the Houtman Abrolhos.

Our analyses at the assemblage level gave some insight into the influences of the Leeuwin Current on the marine plant floras of the Houtman Abrolhos and Jurien Bay regions, using the Dampierian and Flindersian Provinces as benchmarks. The flora of the Houtman Abrolhos showed a slightly greater affinity with the tropical (Dampierian) rather than the temperate (Flindersian) region of Western Australia, while the more southerly located Jurien Bay region was clearly strongly affiliated with the temperate flora. This suggests the Leeuwin Current exerts a greater influence on the algal flora of the offshore Houtman Abrolhos compared to the inshore Jurien Bay region, although it must also be recognised that differences in sampling methods, intensity and objective, as well as the number of species recorded in each region, could be confounding our results. Our choice of the Jurien Bay region as a comparison was based on availability of species records, as comparable data are not available for the more northerly mainland immediately adjacent to the Houtman Abrolhos. Thus it could be argued that our findings simply represent a latitudinal gradient and are not illustrative of the Leeuwin Current's influence. While we acknowledge this, we also point out that a search of the WA Herbarium records (undertaken 16 July 2008) of the tropical species recorded for the Houtman Abrolhos (Table 1) yielded no records of these species on the adjacent mainland, and only two further south (a single record of *Yamadaella caenomyce* at Rottnest Island and several of *Chondria dangeardii* at Jurien Bay). Conversely, records of temperate species are also scant, but several of the examples given above (including *Ecklonia radiata, Hennedya crispa, Caulerpa simplicuiscula* and *Myriodesma quercifolium*) have been found to as far north as Kalbarri (27°42'S). The most northerly mainland record of *Ecklonia radiata* is a drift specimen at Horrock's Beach (28°22'S), further south but closely comparable to the Houtman Abrolhos record at North Island (28°18'S). These observations would suggest that some temperate species, at least, are found at comparable latitudes to the Houtman Abrolhos on the mainland, but no tropical species. However, the records from the region are sparse and often based on drift specimens, so we refrain from drawing any conclusions regarding species distributions. These observations do suggest, however, that our results would not have changed in any way if a more northerly mainland region was included in the analyses. What is also clear is that the marine flora of many regions of the Western Australian coastline is poorly represented in the WA Herbarium, a situation that can only be remedied by increased collecting.

A more robust method of determining the influence of the Leeuwin Current is to consider the taxonomic breadth of each algal region. The measure used in this study, average taxonomic distinctness (Δ^+), is independent of sampling effort and techniques and is an intuitive measure of biodiversity (Clarke & Warwick 2001). In this study, Δ^+ was negatively correlated with increasing latitude. Although latitude itself is not considered a major driver of biodiversity, it is well-documented that the temperature (and therefore influence) of the Leeuwin Current decreases with increasing latitude, due to mixing, radiation and evaporation (Cresswell 1991: Figure 1). The observed decrease in taxonomic breadth moving south along the Western Australian coastline may be, in part, related to the southerly-flowing Leeuwin Current although other environmental factors including habitat diversity (Clarke & Warwick 2001) may play a role. Furthermore, although the Houtman Abrolhos lie within the Flindersian Province with the result that many species are common to both areas, the similarity in Δ^+ values between the Houtman Abrolhos and the Dampierian Province indicate a substantial tropical influence at the former. From this, we conclude that the affinities of the marine algae of the Houtman Abrolhos clearly indicate a transitional zone between tropical and temperate regions, with the strong tropical influence a direct result of the Leeuwin Current. In contrast, the nearby inshore flora at Jurien Bay exhibits a much lower, almost negligible tropical influence. Both Hatcher (1991) and Huisman (1997) recognised the influence of the Leeuwin current on the marine algal assemblages of the Houtman Abrolhos on a broad scale – this is now confirmed by the more detailed analyses undertaken here.

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◀ Figure 4. Marine algae from the Houtman Abrolhos. A. *Asteromenia exanimans* Saunders *et al.*, found at the Houtman Abrolhos and also at Jurien Bay. B. The red alga *Trichogloea requienii*, a widespread tropical species found at the Houtman Abrolhos. C. The green alga *Dictyosphaeria cavernosa* is found in the tropics worldwide and reaches its most southerly distribution in Western Australia at the Houtman Abrolhos. D. The kelp *Ecklonia radiata* growing amongst the coral *Acropora*, one of many unusual associations of temperate and tropical species at the Abrolhos. E–H. Tropical species at their southern limits at the Houtman Abrolhos: E. The red alga *Titanophora pikeana*. F. The green alga *Anadyomene plicata*. G. Another green alga, *Codium geppiorum*. H. The red, sponge-associated alga *Ceratodictyon spongiosum*. I, J. Temperate species at their northern limits at the Houtman Abrolhos: I. The kelp *Ecklonia radiata*. J. The brown alga *Asperococcus bullosus*. (Photos: J. Huisman).

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Influence of the Leeuwin Current on the distribution of fishes and the composition of fish assemblages

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Abstract

Change in the structure of fish assemblages was examined across the 100 km north-south stretch of the Houtman Abrolhos Islands, Western Australia and related to the southward flowing warm Leeuwin Current. Assemblages to the north at Ningaloo Reef and to the south at Rottnest Island were also compared to Houtman Abrolhos assemblages with reference to the Leeuwin current. Fish data was collected at all locations using baited remote underwater stereo-video systems (stereo-BRUVS) in depths of 8–12 m. 105 fish species were surveyed at the Houtman Abrolhos Islands during this study, 21% of these species have a warm-temperate latitudinal distribution, 13% sub-tropical and 66% tropical. Fish assemblages surveyed at the Houtman Abrolhos were distinct from, and somewhat intermediate between, fish assemblages surveyed to the south at Rottnest Island and to the north at Ningaloo. The composition of fish assemblages differed greatly across the four island groups of the Houtman Abrolhos and between sites within each group. While the Houtman Abrolhos fish assemblage is strongly influenced by the Leeuwin current, large small-scale variability in assemblages within and across island groups is likely driven by non-exclusive factors such as the patchiness or complexity of the habitat, predator/prey relationships and competition.

Introduction

Located on the edge of the continental shelf between 28°15'S and 29°S the Houtman Abrolhos is directly influenced by Western Australia's dominant ocean current – the Leeuwin Current (Pearce 1997). The Leeuwin Current flows southward along the West Australian coast bringing warm water from the tropics. Passing directly through the Houtman Abrolhos the current facilitates the existence of the most southern true coral reefs of the Indian Ocean (Veron & Marsh 1988) and a marine ecosystem comprising a high proportion of tropical species (Maxwell & Cresswell 1981; Morgan & Wells 1991; Huisman 1997).

Previous research on fish assemblages of the Houtman Abrolhos includes qualitative taxonomic surveys of fish assemblages (Hutchins 1994; Hutchins 1997a, b; Hutchins 2001), species-specific demographic research (Nardi *et al.* 2006) and assessments of the effects of fishing on reef fish species (Nardi *et al.* 2004; Watson *et al.* 2007). Fish fauna of the Houtman Abrolhos currently totals 389 species, 66% of which are tropical, 19% warm-temperate and 13% sub-tropical (Hutchins 1997a). The majority of tropical species at the islands are in low abundance suggesting that the Houtman Abrolhos relies heavily on the south-ward flowing Leeuwin Current to deliver tropical recruits (Hutchins 1994, 1997b). The Houtman Abrolhos may also be a source of tropical recruits for Rottnest Island some 400 km to the south via the Leeuwin Current (Hutchins 1997b). Not all tropical fish species at the Houtman Abrolhos necessarily rely on the Leeuwin Current for the maintenance of breeding populations. For example, the common and abundant coral trout (*Plectropomus leopardus*), has been shown to be genetically distinct from populations to the north (van Herwerden *et al.* 2006) and therefore appears to be maintaining breeding populations at the Houtman Abrolhos Islands.

The temperate-tropical convergence location of the islands permits co-existence of warm-temperate, sub-tropical and tropical fish species that distinguish the Houtman Abrolhos from adjacent mainland and areas further to the north and south (Hutchins 1994). Less clear is the change in composition of fish assemblages across the latitudinal gradient of the islands themselves which span 100 km from the North Island to the southern Pelsaert group. Here we examine the structure of fish assemblages across the four island groups of the Houtman Abrolhos and discuss differences between the islands assemblages to those studied to the south at Rottnest Island and to the north at Ningaloo using the same sampling technique.

Materials and Methods

Sampling Design

Surveys were conducted from May 17th–22nd, 2007 at the four island groups of the Houtman Abrolhos; Pelsaert, Easter, Wallabi and North (Figure 1). At each

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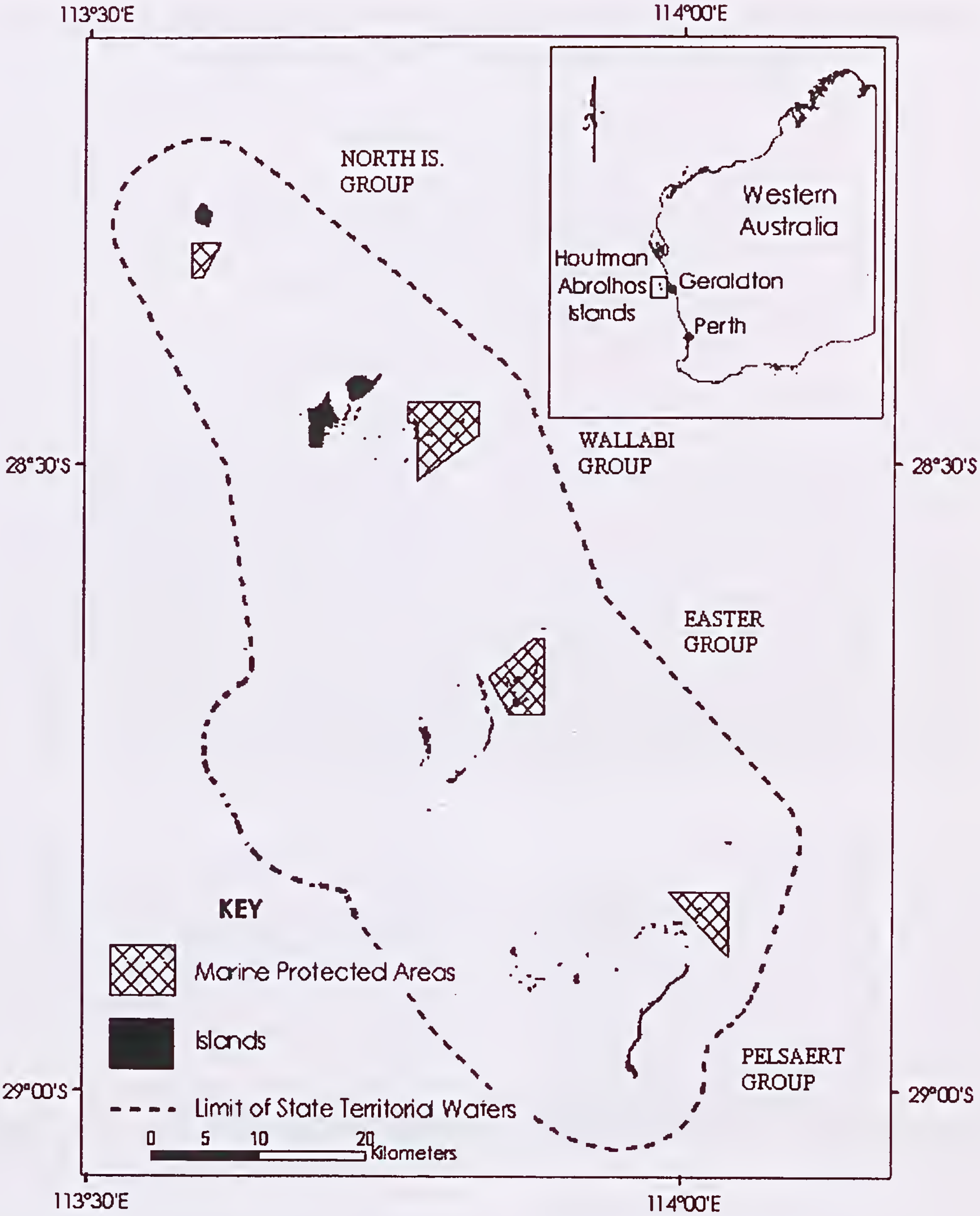

Figure 1. Map of the Houtman Abrolhos Islands.

island group, fish were surveyed on shallow reef slopes (8–12 m depth) at three randomly located areas separated from each other by hundreds to thousands of metres. All locations were of similar high exposure, bordering deep channels or on the edge of large islands exposed to the open ocean. Sampling was standardised by habitat with all surveys conducted along reef slopes where habitat was predominantly branching and plate *Acropora* spp. Five replicate samples were collected at each of the three locations for each island group.

Fish assemblages at Rottnest Island and at Ningaloo have also been surveyed using the same technique at similar depths. Therefore, we were able to compare fish assemblage composition at the Abrolhos to the composition of assemblages 750 km to the north at Ningaloo (latitude 22°) (B Fitzpatrick & E Harvey unpubl. data) and 400 km to the south at Rottnest Island (latitude 32°) (WA Marine Futures unpubl. data). Note that sampling effort was not equal between the locations with only 19 sites from Rottnest and 11 sites from Ningaloo included in comparisons to the Abrolhos (60 sites).

Sampling technique

Baited remote underwater stereo-video systems (stereo-BRUVS) were used to survey fish assemblages

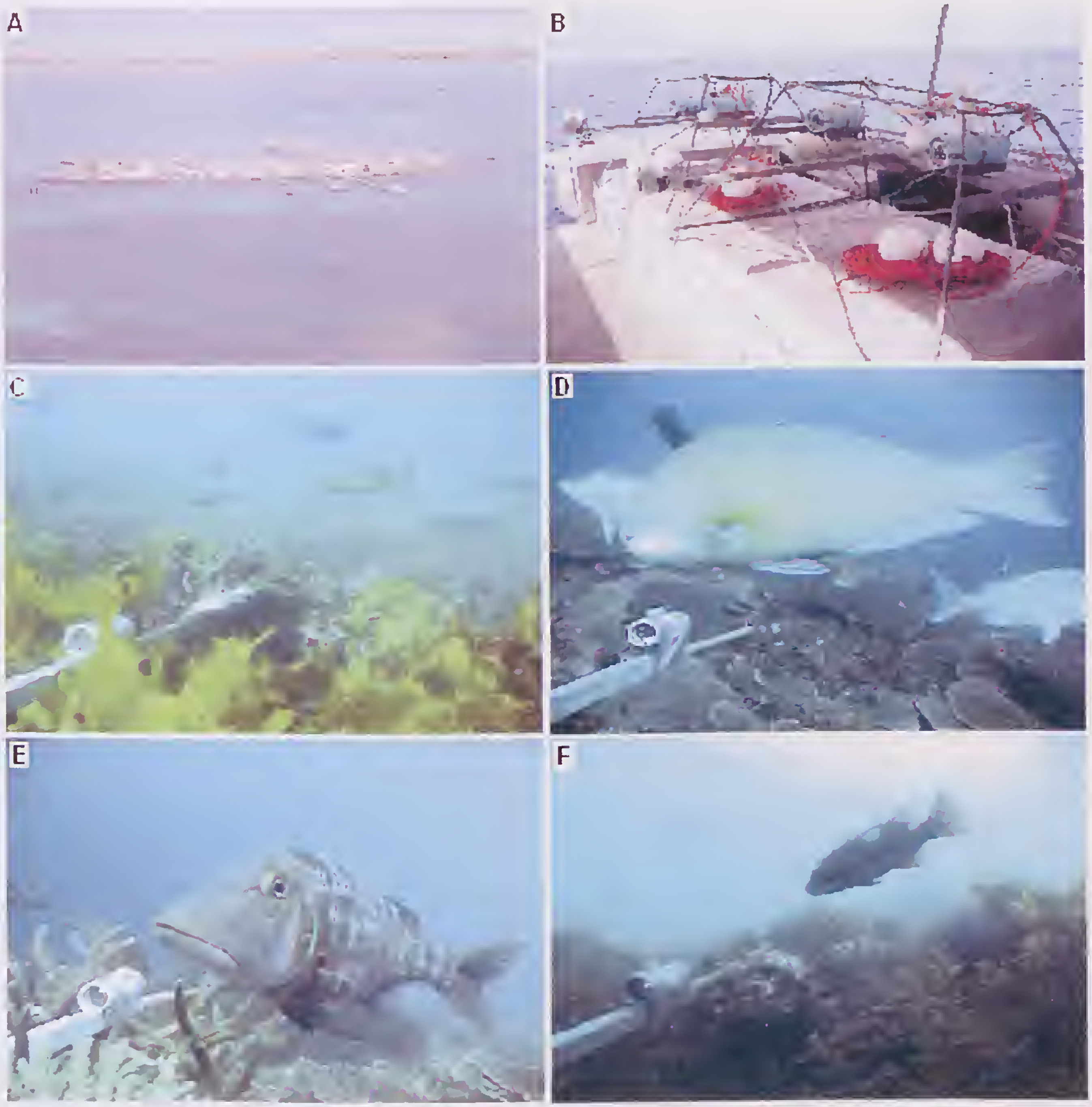

Figure 2. Selection of images from the Houtman Abrolhos Islands. A) A typical inhabited island with rock lobster fishers camps; B) stereo-BRUV camera setup; C) the tropical coral trout, *Plectropomus leopardus* amongst staghorn coral and kelp; D) the sub-tropical baldchin groper, *Choerodon rubescens;* E) the tropical redthroat emperor, *Lethrinus miniatus;* F) the temperate western foxfish, *Bodianus frenchii.*

(Figure 2B). Detailed information on their design, use and measurement accuracy can be found in the literature (Harvey & Shortis 1996; Harvey *et al.* 2001a, b, 2002, 2004). Simply, the stereo-BRUV systems are comprised of two SONY HC 15E video cameras in water-proof housings, mounted 0.7 m apart on a base bar inwardly converged at 8 degrees to gain an overlapping field of view (Harvey & Shortis 1996). Research has shown that in addition to species expected to visit baited stations, stereo-BRUVs also survey prey and herbivorous species, some cryptic crevice dwelling species (*e.g.*, Muraenidae, Pseudochromidae spp.) and transient species (*e.g.*, Scombridae) (Watson *et al.* 2005, 2007; Harvey *et al.* 2007). Other advantages of the technique relevant to this study include; storage of footage for fish identification, safety in the field (no SCUBA) and rapid field sampling (Watson *et al.* 2007). The present study used 8 stereo-BRUV systems such that each could be deployed by boat, one after the other, at separate sites. After one hour (max tape recording time) the first would be retrieved and re-deployed then the second retrieved, re-deployed, and so on, facilitating high sampling efficiency. The bait consisted of 800 grams of pilchards (*Sardinops sagax)* in a plastic-coated wire mesh basket that was suspended in front of the two cameras. The pilchards were crushed to maximise bait dispersal. Adjacent replicate deployments were separated by 250–400 m to ensure similar coral cover while reducing the likelihood of fish moving between each stereo-BRUV within the sampling period. Temperate loggers (TidbiT v2) were attached to each of the eight stereo-BRUV frames to obtain *in situ* measures of temperature. The loggers were set to record temperature every 10 minutes providing 6 measures for each deployment.

In the laboratory, video images of each site were reviewed and all fish observed were identified to species and catalogued using the software program EventMeasure (SeaGIS 2008). EventMeaure, in addition to other measures, permits the relative abundance of every species to be logged. These relative abundance counts are known as 'MaxN', *i.e.*, the maximum number of fish belonging to each species, present in the field of view of the cameras at one time (see also Priede *et al.* 1994; Willis & Babcock 2000; Cappo *et al.* 2004). By using MaxN we avoid repeatedly sampling a single individual. It is often the case that only a portion of fish will be visible at one time and therefore MaxN is a conservative estimate of the number of fish in the vicinity of the cameras.

The percent cover of different habitat types was estimated from freeze-framed video images for every site. This measurement was made by visually estimating what percent of the total field of view of the substrate each habitat type occupied. Seven common and broad habitat types were often observed on video images. These habitat types included; staghorn coral (branching *Acropora* spp.), plate coral (plate *Acropora* spp.), other coral species, kelp (*Ecklonia radiata;* Figure 2C), other algae (usually *Sargassum* spp.), sand and coral rubble.

Statistical Analyses

The experimental design consisted of two factors: island group (four levels, fixed: Pelsaert, Easter, Wallabi and North) and site (nested in island group, random with three levels). One hundred and five fish species were included in the multivariate analyses. The multivariate data set was analysed using permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) in the Primer-E software package. This permutational distance-based approach was used for analyses because the relative abundances of fish were highly skewed and contained many zero counts. All multivariate analyses were conducted using the Modified Gower log base 10 dissimilarity matrix on raw untransformed relative abundance data. Analysis of percent cover of habitat types was conducted in a similar manner but instead using Euclidean distance on arcsine transformed percentages. Furthermore, the habitat types (arcsine percentages) were included as covariables in the PERMANOVA analysis on relative abundance data. The contribution of habitat and temperature to variation in fish assemblages was examined using DISTLM (distance-based multivariate analysis for a linear model; McArdle & Anderson 2001). A canonical analysis of principal coordinates (CAP; Anderson & Robinson 2003; Anderson & Willis 2003) was also conducted on relative abundance data to examine whether fish assemblages could be discriminated across the four island groups. Individual species likely to be responsible for any observed differences between island groups were determined by examining Pearson correlations of species counts with canonical axes. A correlation of $|r| > 0.3$ was used as an arbitrary cut-off to display potential relationships between individual species and the canonical axes. Fish assemblages from Ningaloo and Rottnest Island were compared to the fish assemblage at the Abrolhos Islands using the PERMANOVA procedure described above with a single factor; location.

Results

Rottnest Island, Ningaloo and the Houtman Abrolhos each have distinctly different fish assemblages (Figure 3; $p < 0.01$, allocation success 100%). Of the 105 fish species surveyed at the Abrolhos, 21% have a warm-temperate latitudinal distribution, 13% sub-tropical and 66% tropical. At Rottnest Islands 91% of the fish species surveyed (53 species) have a warm-temperate distribution, 7% sub-tropical and 2% tropical. Of the 83 species surveyed at Ningaloo, none had a warm-temperate distribution, 8% were sub-tropical and 92% tropical. 23 species were common to Rottnest Island and the Houtman Abrolhos and 37 species were common to the Abrolhos and Ningaloo. Only a single species was recorded at all three locations, the moon wrasse *Thalassoma lunare.*

Stereo-BRUV surveys of fish assemblages across the four island groups of the Houtman Abrolhos recorded 5645 individuals from 105 species and 32 families with 14 species being endemic to Western Australia (13.3%). The ten most common fish species observed on stereo-BRUV images include; *Plectropomus leopardus* (Figure 2C), *Choerodon rubescens* (Figure 2D), *Pomacentrus milleri, Scarus schlegeli, Coris auricularis, Thalassoma lutescens, Thalassoma lunare, Lethrinus miniatus* (Figure 2E), *Labracinus lineatus* and *Pagrus auratus.*

From stereo-BRUV images the 7 habitat categories varied greatly at the smallest level of sampling (Site; d.f. = 8,59; MF = 5957.4; Pseudo F = 2.29; $p = 0.001$). Similarly, water temperature also varied at the site level (d.f. = 8,59; MF = 1.19; Pseudo F = 3.13; $p = 0.006$). Neither habitat or temperature differed significantly across the four island groups (all $p > 0.05$). Of the 7 habitat categories, 4 had a significant effect on the variation in fish assemblages; branching *Acropora* spp., plate *Acropora* spp., other coral species and sand (all $p < 0.04$). Together, habitat and temperature accounted for 21.6% of the variation in the relative abundance of fishes. On its own temperature only accounted for 1%. The inclusion of habitat as a covariable in the PERMANOVA analysis showed that habitat, although highly variable across sites, did not contribute to differences in fish assemblages across any levels of the model (non-significant interaction values; Table 1). Relative abundances of all fish species and families differed significantly across the four island groups (Table 1). Pairwise comparisons could not identify which island groups were driving this significant group effect (all $t < 2.3$; $p > 0.05$). PERMANOVA on latitudinal groups (species summed to warm-temperate, sub-

Table 1

PERMANOVA based on Modified Gower log base 10 dissimilarities of relative abundances of 105 fish species in response to habitat covariables (CO), island group (Gr), sites (Si) and their interactions.

		105 species variables			32 Family variables		
Source	**df**	**MS**	**Pseudo-F**	**P(perm)**	**MS**	**Pseudo-F**	**P(perm)**
CO	7	1.01	1.86	0.06	1.14	2.54	0.02
Gr	3	1.01	1.49	0.05	1.02	1.77	0.05
Si(Gr)	8	0.68	1.41	0.16	0.58	1.46	0.19
COxGr	15	0.49	1.02	0.49	0.41	1.03	0.48
COxSi(Gr)	14	0.43	0.90	0.69	0.42	1.07	0.42
Res	12	0.48			0.39		
Total	59						

Table 2

Allocation success of replicates to island groups (# correct out of 15) for fish data. Note that with four groups a 25% success rate would be expected if results were no better than random.

Island Group	# correct	Allocation success (%)
Pelsaert	11/15	73
Easter	10/15	67
Wallabi	11/15	73
North	13/15	87

tropical or tropical) found no significant differences across island groups ($p = 0.75$).

Similar to PERMANOVA, a CAP analysis on species data showed fish assemblages differed across the four island groups ($p = 0.002$; Figure 4). Canonical axes separated fish assemblages present at each of the island groups well, with no overlap. This distinctiveness of the assemblages at each island group was illustrated by leave-one-out allocation success rates from the CAP analyses that were >67% (Table 2). When species were summed to families and to latitudinal groups, CAP also found a difference between island groups (both $p < 0.01$). At the family level, allocation success rates were low with 46% for the Wallabi group, 60% for the Easter and North group and 66% for the Pelsaert. For latitudinal groups, allocation success rates were lower still with only 6% of sites correctly assigned to the Wallabi group, 40% to North Is, 53% to the Easter group and 60% to the Pelsaert group. Therefore, at the family and latitudinal group level, assemblages showed greater overlap across island groups particularly at the two northern groups.

17 species were identified by CAP as having a strong Pearson's correlation with canonical axes that separated island groups. Associated with the North Island were; *Apogon angustatus, Chromis westaustralis, Lethrinus atkinsoni, Lethrinus nebulosus* and *Lethrinus sp.* Associated with the Wallabi group were; *Coris auricularis, Lethrinus miniatus, Scarus ghobban* and *Thalassoma lunare*. Fish species associated with the Easter group included; *Bodianus frenchii, Chaetodon assarius, Chaetodon lunula, Chlorurus sordidus, Dascyllus trimaculatus* and *Labracinus lineatus*. Finally, species associated with the Pelsaert group were *Gymnothorax woodwardi* and *Scorpis*

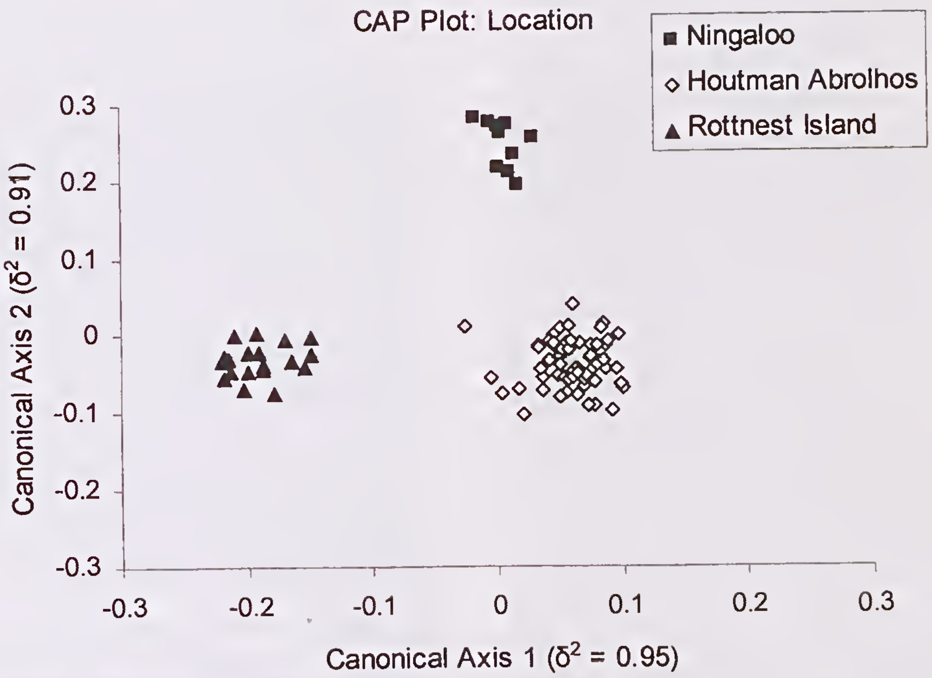

Figure 3. Canonical analysis of principal coordinates (CAP) ordination for locations.

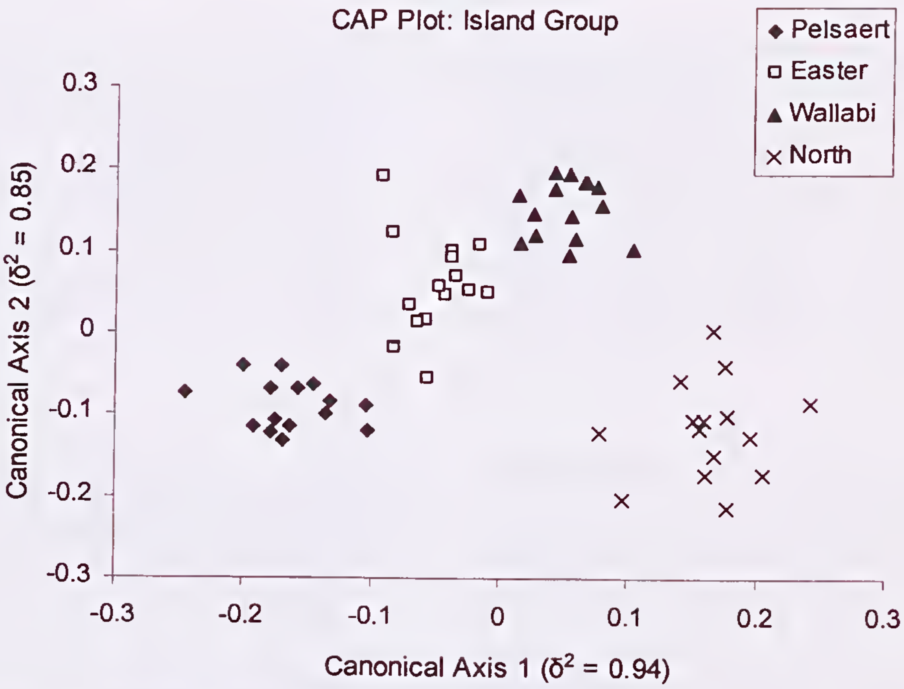

Figure 4. Canonical analysis of principal coordinates (CAP) ordination for island group.

georgianus. Many of the most common and abundant species viewed on video images were present at all island groups, *e.g.*, *Plectropomus leopardus, Pomacentrus milleri, Choerodon rubescens, Pagrus auratus, Thalassoma lutescens* and *Scarus schlegeli*. Because the distinction between island groups was not as pronounced at the family level, only several families of fish exhibited correlations to particular island groups. The families Muraenidae and Serranidae were associated with the Pelsaert group while Scaridae and Chaetodontidae were associated with the Easter group.

Discussion

The Leeuwin current is thought to strongly influence the structure of fish assemblages with many fish species likely relying on recruitment from more northern populations via the southward flowing current (Hutchins 1997b). While fish assemblages at the Houtman Abrolhos comprise mostly tropical fish species, numbers of tropical species are low compared to assemblages further to the north around Ningaloo (see also Hutchins 1994). This impoverished tropical diversity is reflective of the temperate-tropical overlap location of the Houtman Abrolhos. Compared to Rottnest Island which is 400 km to the south, the Houtman Abrolhos have a much higher proportion of sub-tropical and tropical fish species. Tropical fish species at Rottnest may have travelled there via the Leeuwin Current from the Abrolhos Islands (Hutchins & Pearce 1994).

Hutchins (1997a) recorded 389 fish species across the Pelsaert, Easter and Wallabi groups, significantly more that what was recorded here (105 species) from the four island groups. The difference is most likely a result of sampling effort and techniques where Hutchins (1997a) used a combination of observational (underwater visual census) and destructive (spearing, trawls, handnets and rotenone) techniques. Despite the comparatively low number of fish species recorded using stereo-BRUVs, a number of species were observed for the first time at the islands; *Naso brevirostris, Pterocaesio digramma, Hemigymnus fasciatus* and *Pentapodus nagasakiensis*. These species are all tropical and may have recruited to the islands in 2000 when the Leeuwin Current was particularly strong (B Hutchins *pers comm.*). With greater sampling effort at the islands using a range of techniques we predict that a large number of species will be reported for the first time. Our findings support those of Hutchins (1997a) in suggesting that any change to the south-ward flowing Leeuwin Current would have an enormous impact on fish assemblages at the Abrolhos Islands.

Given the temperate-tropical transitional location of the islands and the southward flowing warm Leeuwin Current, one would expect a gradual decline in the number of tropical fish species from the North Is. to the Pelsaert group some 80–100 km to the south. Indeed a number of tropical fish species did exhibit this trend (*Lethrinus miniatus* (Figure 2E), *Lethrinus nebulosus, Lethrinus sp* and *Thalassoma lunare* associated with the North Is.*)*. Furthermore, a number of temperate species were highly associated with the more southern island groups (*Scorpis georgianus, Gymnothorax woodwardi, Bodianus frenchii;* Figure 2F). For the majority of fish species, however, their distribution did not appear to be related to latitudinal location. Our data suggest that while the Leeuwin Current strongly impacts the composition of fish assemblages at the Abrolhos, the southward flowing current does not appear to strongly influence the distribution of fish species across the four island groups. Seasonal and more extensive studies, however, would need to be conducted to further examine this.

High variability in fish assemblage structure at the smallest scale of sampling (between sites) could be a caused by a number of factors including; food availability, competition, exposure, available habitat, predator/prey relationships and fishing pressure. Furthermore, the presence of fish species in particular areas may also vary with age and ontogeny (Forrester 1991; Clements & Choat 1993; McCormick 1998; St John 1999). Several habitats did have a significant influence on variability in fish assemblages (categories: branching *Acropora* spp, plate *Acropora* spp, other macroalgae and sand). This influence, however, was not sufficient to explain observed differences in assemblages across sites or island groups. Habitat and temperature, while also highly variable at relatively small spatial scales, explained 21% of the variability in fish assemblages. Examination of habitat from video images is very restrictive however, and measures rely strongly on the orientation of the cameras. Links between habitat types observed on video footage and fish assemblages in the area would likely have been stronger if bait was not used. By using bait we are attracting mobile fish species into the field of view of the cameras and for some species they may be drawn away from their preferred habitat. Benthic habitat surveys which characterise habitat presence, extent and rugosity, in combination with fish surveys (stereo-BRUVS and underwater visual census techniques) would provide a much better insight into fish-habitat relationships at the Houtman Abrolhos Islands.

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El Niño Southern Oscillation and the Leeuwin Current influence on seabird reproductive performance and diet at the Houtman Abrolhos

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Abstract

Each spring/summer over a million pairs of seabirds breed at the Houtman Abrolhos, Western Australia, Eastern Indian Ocean. The southward flowing Leeuwin Current is the main oceanographic feature influencing this location. Seabirds are reliant wholly upon marine sources of food, and several species feed predominately upon larval ichthyoplankton species, the availability of which has been found to play a pivotal role in their reproductive parameters. The timing of breeding, breeding participation and reproductive success were investigated in two tern species, the Lesser Noddy and Brown Noddy, at the Houtman Abrolhos between 1991 and 2006. The diet of these two species was investigated from 1991–2000. Life history traits determined the response of these seabirds to fluctuations in marine resources through variation in the flow of the Leeuwin Current. During ENSO events, when the Leeuwin Current flowed more weakly and the Southern Oscillation Index had been low, reproductive effort and output was severely reduced for these two tern species. These conditions appeared to result in low prey availability, which delayed the commencement of seabird breeding by up to two months and caused catastrophic breeding failures. The long-term data set would indicate that the interaction of other oceanographic factors at the Houtman Abrolhos, such as eddies, the Cresswell and Capes Currents, in conjunction with the Leeuwin Current, may influence seabird prey availability, however the dynamics of these interactions are not yet understood. The use of seabirds as an upper trophic- level indicator of changes in marine productivity, as a result of variability in the Leeuwin Current and other oceanographic factors, is discussed.

Introduction

The main oceanographic feature of the Western Australian coastline is the Leeuwin Current. This is a body of warm (>24°C), low-salinity (<35‰) water which flows southward along the continental shelf of Western Australia, in a broad and shallow band (200km wide by 50m depth) at speeds of up to 2 km.h^{-1} (Cresswell 1990; Pearce 1991). The strength of the flow of the Leeuwin Current varies both annually in its cycle as well as seasonally. The greatest flow occurs in winter, between April and July, and its strength and temperature is affected by El Nino Southern Oscillation (ENSO) events. ENSO events are measured using the Southern Oscillation Index (SOI), which is based on the difference in atmospheric pressure between Tahiti, in the Pacific, and Darwin in northern Australia (Pearce 1991). In ENSO years the Leeuwin Current is weaker, resulting in cooler, more saline water along the outer continental shelf (Pearce 1991). Higher sea levels and warmer sea temperatures occur along the Western Australian coastline during non-ENSO years, resulting in the Leeuwin Current having a stronger southward flow (Cresswell *et al.* 1989). Reduced breeding participation and reduced breeding success has been observed in seabird colonies along the WA coastline, ranging between 19°S and 32°S, during seasons influenced by ENSO events (Dunlop *et al.* 2002; Nicholson 2002; Surman 1997).

The Houtman Abrolhos is located at 28°S (Figure 1) and contains one of the southernmost extensions of tropical marine flora and fauna in the Indian Ocean principally due to the influence of the Leeuwin Current. The Leeuwin Current transports pelagic larvae of corals, fishes, crustaceans and molluscs from tropical northern waters to the surrounding waters of the Houtman Abrolhos and further south to Rottnest Island (32°S), and in response to this influx, there has been a corresponding southwards shift in tropical seabird breeding populations to new higher latitude colonies in the past 50 years (Dunlop & Wooller 1990). This has included the colonisation of Rottnest Island by Wedge-tailed Shearwaters *Puffinus pacificus* in the 1940's (Serventy *et al.* 1971), the continued expansion of a Bridled Tern *Sterna anaethetus* colony on Penguin Island (Dunlop & Jenkins 1994), the discovery of Bridled Terns foraging offshore of the Recherche Archipelago in 1993 (Surman & Wooller 2000) and their consequent colonisation (Dunlop pers. comm.), and the establishment of a new colony of Brown Noddies *Anous stolidus* and Sooty Terns *Sterna fuscata* on Lancelin Island (Dunlop & Mitchell 2001). The role of the Leeuwin Current in the delivery and distribution of seabird ichthyoplankton prey at the Houtman Abrolhos remains unclear but well-established relationships exist between Leeuwin current strength and

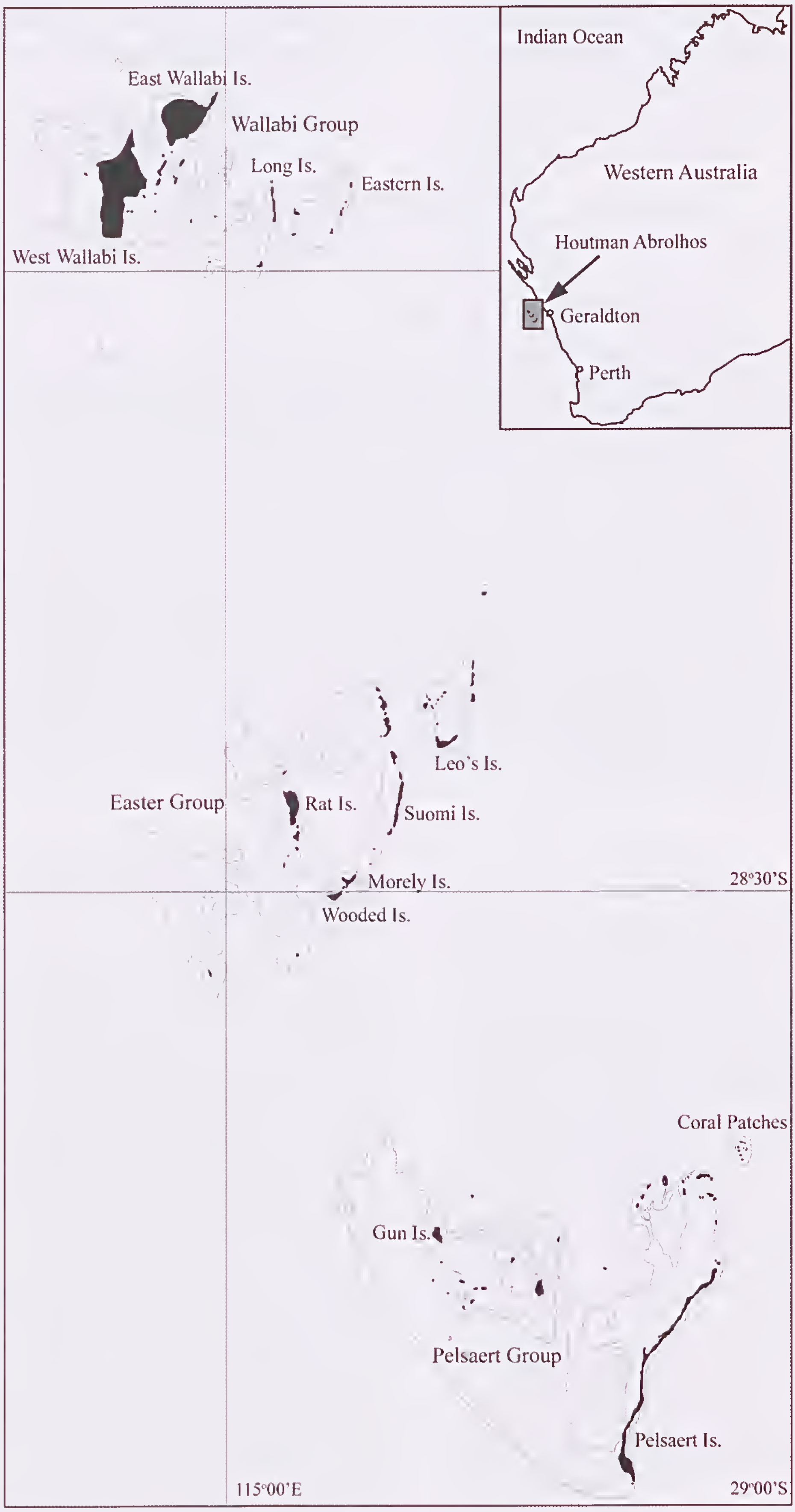

Figure 1. Location map of the Houtman Abrolhos, Western Australia.

western rock lobster (*Panulinus cygnus*) recruitment (Caputi *et al.* 2001; Caputi 2008).

Many of the seabirds which breed at the Houtman Abrolhos are considered predominantly tropical and breed annually during the austral spring-summer (Surman 1998). Most studies agree that seabird breeding is specifically timed to coincide with maximal food supply (Ashmole & Ashmole 1968; Diamond 1983; Ainley & Boekelheide 1990). This timing varies with latitude, with high-latitude species having a narrower period of opportunity to breed due to strong seasonality in climate and food availability and so are characterized by predictable breeding times, high synchrony and relatively short breeding seasons (considered here from the time of laying to fledging of young, excluding prelaying and postfledging periods). At lower latitudes, however, breeding at some locations may commence at any time, and timing is only determined by the availability of food in reach of the colony (Ashmole & Ashmole 1968; Diamond 1983). At the Houtman Abrolhos seabirds breed annually and commence during the spring/summer period (Surman 1998). The Houtman Abrolhos can be considered a sub-tropical location due to the influence of the Leeuwin Current, and as such provides breeding seabirds with a mixture of tropical and temperate prey sources (Surman & Wooller 2003). Two terns which breed at the Houtman Abrolhos, the Lesser Noddy *Anous tenuirostris* and Brown Noddy, share breeding times of between 75–85 days. The former is a resident species of the Houtman Abrolhos for most of the year, while the larger Brown Noddy is a migratory species, returning to the region in August of each year from northern parts of the Eastern Indian Ocean.

This paper investigates inter annual variability in the breeding performance and phenology of the Lesser and Brown Noddy, and the influence that regional oceanography may have upon the diet of these species, in relation to the Leeuwin Current dynamics.

Methods

Study area and species

The study was conducted on Pelsaert Island (28°56'S, 113° 58'30"E), the southernmost and third largest of an archipelago of 192 islands, islets and rocks (the Houtman Abrolhos), 60 km off the mid-western coast of Australia (Figure 1). Pelsaert Island (120 ha) is 12 km long, 50–500 m wide, up to 2 m above sealevel, comprising coral rubble, limestone and sand. The Lesser Noddy (35,000 pairs) nests mainly in branches of the White Mangrove *Avicennia marina* on the island and the Brown Noddy (130,000 pairs) nests on low Nitre *Nitraria billardierei* and Samphire *Halosarcia halocnemoides* bushes (Surman & Wooller 1995, 2000; Surman & Nicholson 2008). At the Houtman Abrolhos, Pelsaert Island contains 100% of Brown Noddies and 70 % of Lesser Noddies breeding along the Western Australian coastline.

Nest sites of the Lesser Noddy and Brown Noddy were selected at random and permanently marked in 1991 and 1993 respectively, for each species. Their contents were recorded weekly over the spring summer period (September–May) between 1991–2001, and in more recent years (2002–2006) during several shorter visits between October and January of each year.

Timing of Breeding and Reproductive Performance

Laying chronology was determined using lay dates of known age eggs, and the estimated laying dates of other eggs was determined by backdating, using the egg water loss techniques (Wooller & Dunlop 1980; Surman & Wooller 1995). Eggs known to be "re-lays" (a second egg laid in the same nest after the first has been damaged or predated) were excluded from calculations for the mean date of laying of each species. In years limited to shorter duration field visits, we were able to determine the timing of breeding from measurement of chicks or eggs at the permanently marked nest sites of the two noddy species.

As a measure of reproductive performance we used breeding success, or the proportion of all active breeding attempts that survived to produce a fledgling. We arbitrarily assigned those seasons when breeding success was less than 15% overall for each study species as "bad", and above 15% as "good".

Environmental parameters

Measures of oceanographic factors between 1991–2006 were obtained from the National Tidal Facility, Flinders University. The strength of flow of the Leeuwin Current was determined by using the mean monthly sealevel at Fremantle and Geraldton, Western Australia. Sealevel is considered a proxy for determining the strength of the Leeuwin Current (Pattiaratchi 2005). Mean monthly Sea Surface Temperature (SST) was obtained from the Reynold's database for the degree squares centred at 28.5°S and 113.5°E and 114°E. The mean monthly Southern Oscillation Index (SOI), an indicator of El Nino activity, was obtained from the Bureau of Meteorology.

Dietary samples

Lesser Noddies and Brown Noddies were induced to regurgitate without the use of emetics or stomach flushing. Although spontaneous regurgitations may not always empty the proventriculus (Duffy & Jackson 1986), this method was judged minimally intrusive and is commonly used to determine seabird diet (Cooper & Klages 1995; Croxall *et al.* 1997; Shealer 1998). Adult birds recently returned from a foraging trip were captured at the nest-site by hand or using a small net, whereupon most regurgitated. They were marked individually with leg bands to ensure that no individual was sampled more than once during any single breeding season. A minimum of 10–20 regurgitations were collected from each species in each sampling month, corresponding to the incubation, small nestling and large nestling stages in their breeding cycle.

Regurgitates were preserved in 70% ethanol, then rinsed and vacuum-filtered to allow the percentage volumes of identifiable material to be estimated before obtaining the wet mass of each sample. The total number of individuals of each prey type in each sample was recorded. Prey items were identified using keys (Last *et al.* 1983; Leis & Rennis 1983; Smith & Heemstra 1986; Leis & Trnski 1989; Gommon *et al.* 1994) and from reference specimens in the Western Australian Museum.

Head parts were poorly preserved in most samples and tails were the most effective method of identifying and counting each species. Of the three main prey species, Beaked Salmon *Gonorhynchus greyii* resisted digestion better than the more fragile Black-spotted Goatfish *Parupeneus spirulata*; Hawaiian Bellowfish *Macrorhamphosus scolopax* remained more intact than either. Fortunately, the tails of these three species proved particularly distinctive.

Results

Timing of Breeding

Figure 2 shows the date (Julian, where 300 = 27 Oct) of first eggs laid and the mean lay date in the Lesser Noddy (A) and Brown Noddy (B), in comparison with the SOI (C), sea level at Geraldton and Fremantle (D) and SST of south-western waters (E) over a 16 year period, from

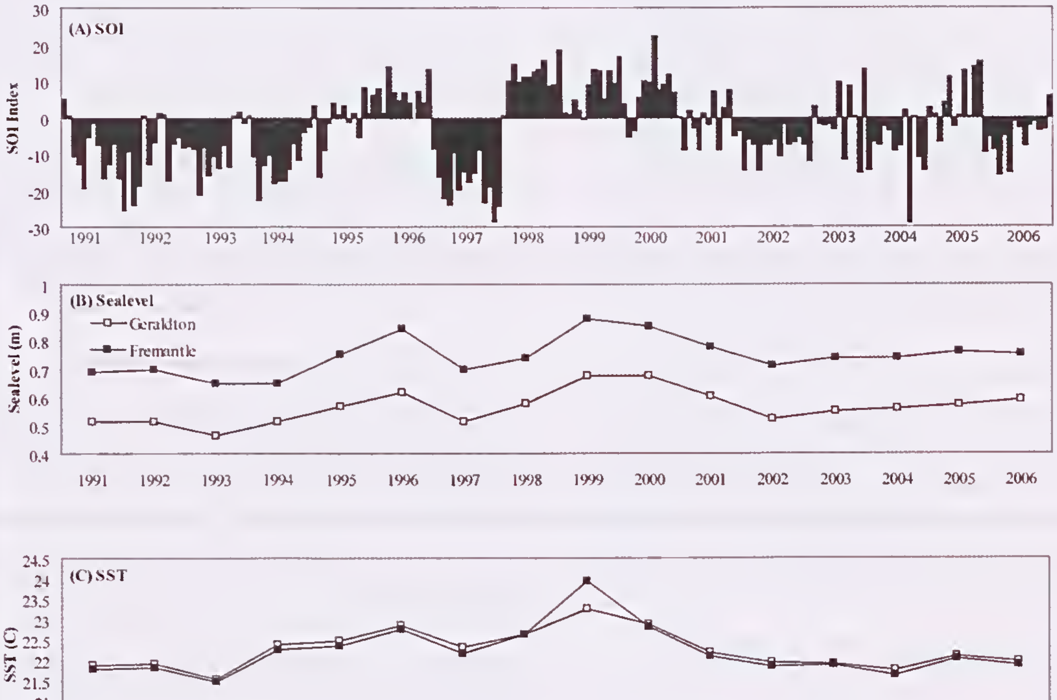

Figure 2. Timing of breeding (Julian Date, where 27 October = 300) as represented by the date of first egg (closed diamonds) and mean lay date (open squares) in the Lesser Noddy (D) and Brown Noddy (E). The Southern Oscillation Index (A) and sealevel (B) at Geraldton (open squares) and Fremantle (closed squares), and the Sea Surface Temperature (C – °C) centred at 28.5°S and 113.5°E (open squares) and 114.5°E (closed squares). Negative SOI values indicate ENSO conditions.

1991–2006. Later breeding coincided with stronger ENSO (negative SOI values) events, lower sea levels and cooler SST. The timing of egg laying in the two noddy species was increasingly delayed until the 1997 ENSO event, after which it returned to an earlier start. This coincided with the SOI becoming positive once again.

During this 16 year period, delayed breeding was accompanied by a decline in the proportion of birds participating in that year (Table 2). The commencement of breeding ranged from late August (in those years when the SOI was positive) to late December (in those years when the SOI was negative).

Diet

Analysis of over 3500 regurgitations (48 000 items) revealed that both the Lesser Noddy and Brown Noddy favoured Beaked Salmon *Gonorynchus greyii* (Table 1, for details see Surman & Wooller 2003), which appeared to be predominately available earlier in the breeding season, particularly during ENSO years. In general, Lesser Noddy regurgitates consisted mostly of Black-spotted Goatfish and Beaked Salmon, whilst Brown Noddy regurgitates were dominated by Beaked Salmon and cephalopods.

Figure 3 shows the relationship between the proportion of beaked salmon and black-spotted goatfish items in the diet during reproductively successful and unsuccessful years. Figure 4 shows pooled data for the ten years of dietary data collected from Brown and Lesser Noddies from the Pelsaert Island colonies. In reproductively good years, the volume of beaked salmon collected from regurgitates in the early portion of the season was very high (70%), dropping off later in the season to about 50%. During poor years, the volume was very low (18%) rising gradually to 40% in the latter part of the breeding season.

Table 1

Main prey items identified in regurgitates from the Lesser Noddy and Brown Noddy from Pelsaert Island, Houtman Abrolhos between 1991 and 2001.

Prey (% Volume)	Lesser Noddy	Brown Noddy
Beaked Salmon	46	69
Black-spotted Goatfish	27	1
Hawaiian Bellowfish	8	8
Squid	3	10

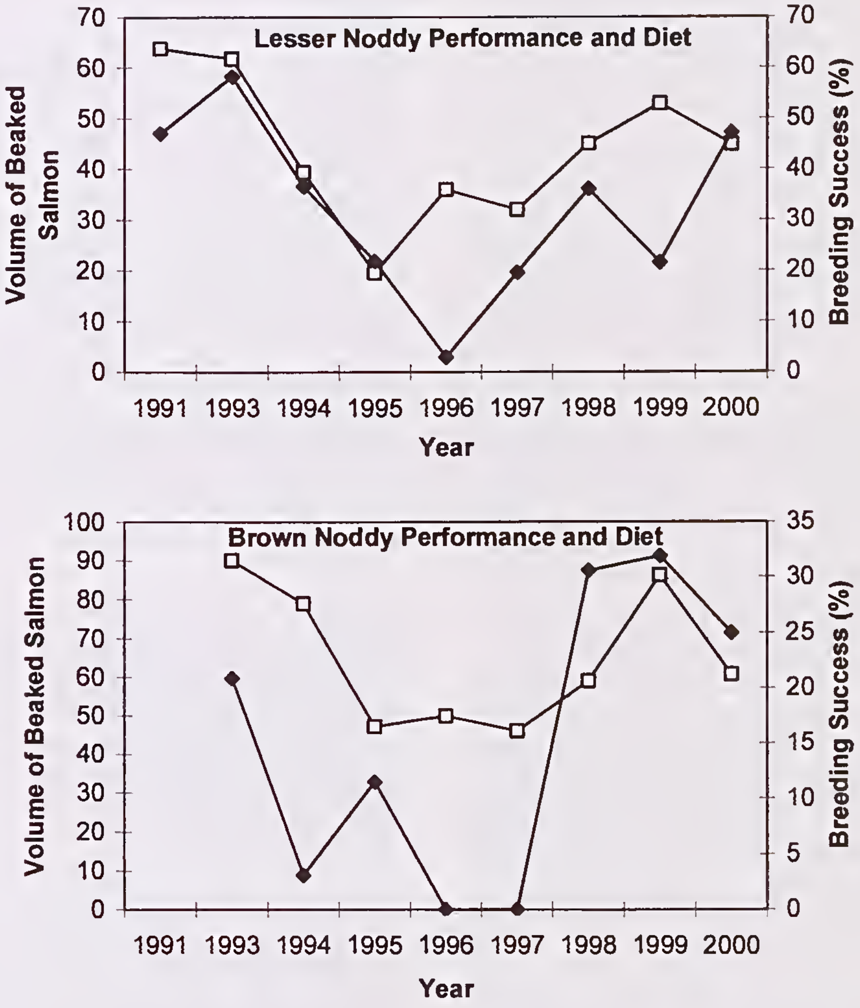

Figure 3. The volume of beaked salmon found in regurgitates (left hand side-open squares) and the breeding success (right hand side-closed diamonds) of the Lesser Noddy (top) and Brown Noddy (bottom) over nine years that dietary data was collected at Pelsaert Island, Houtman Abrolhos.

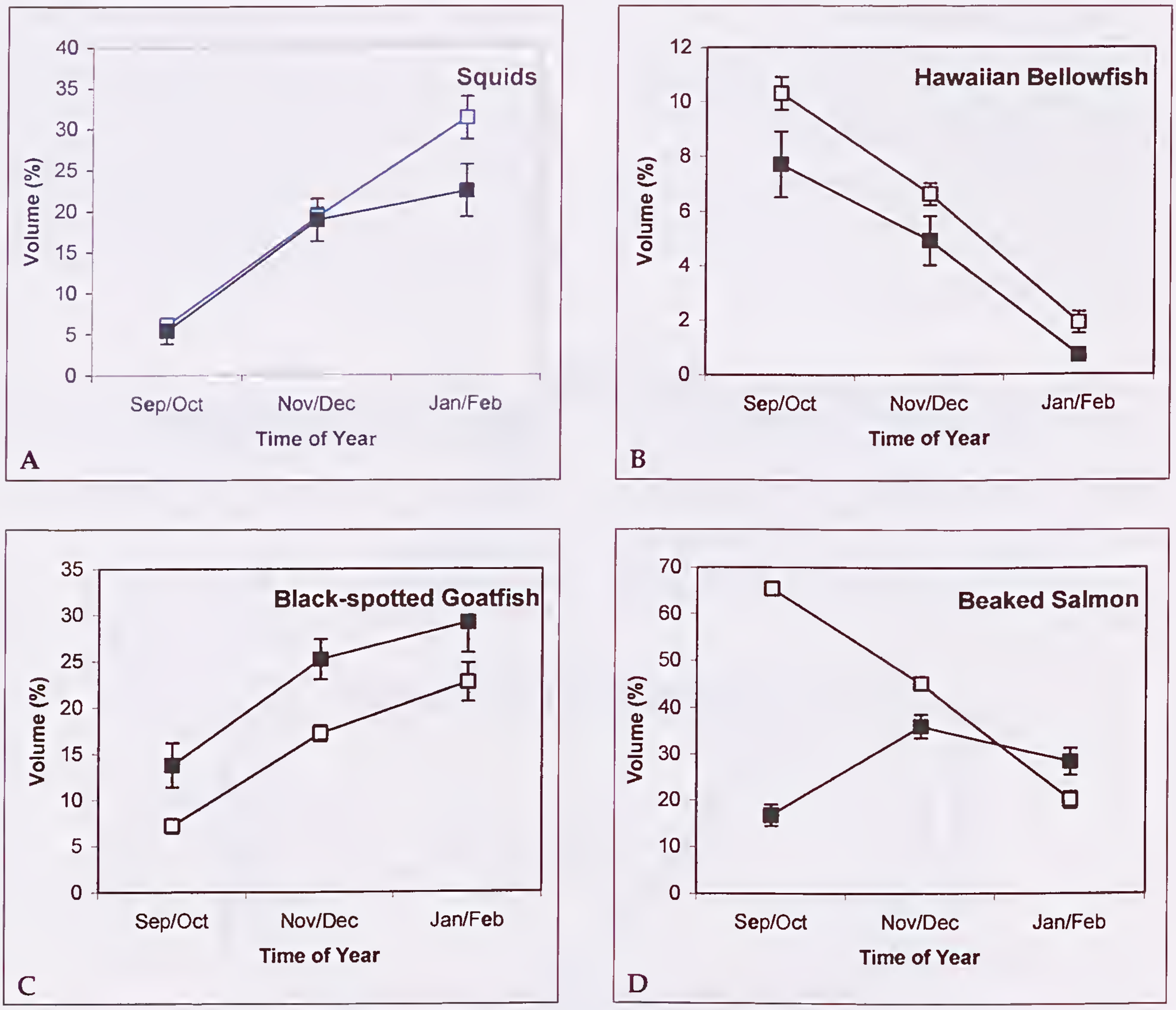

Figure 4. Pooled seasonal dietary data for Lesser and Brown Noddies at Pelsaert Island, Houtman Abrolhos between 1993–2001. The figures represent the four key prey items consumed by these species, (A) Squids, (B) Hawaiian Bellowfish, (C) Black-spotted Goatfish and (D) Beaked Salmon. Open squares represent dietary data from reproductively successful years and closed squares from reproductively poor years.

The residential Lesser Noddy was less reliant upon Beaked Salmon than the migratory Brown Noddy. This was reflected in the reproductive performance of the two species in ENSO years, as the Lesser Noddy was buffered by its ability to take advantage of the small larval Black-spotted Goatfish later in the season, whereas the Brown Noddy required a much higher proportion of Beaked Salmon throughout the season, and on average faired worst (Table 2, Figure 3). For Brown Noddies the population suffered a complete reproductive failure in those years when the proportion of Beaked Salmon in diet fell below 50 % by volume (Figure 3).

Breeding Success

Breeding success, defined as the proportion of young raised to fledging age, was dramatically reduced in years of strong ENSO events (Figure 3). The delayed commencement of breeding in these years resulted in chicks being reared very late in the season when prey availability was already declining (Table 2). In 1997, 2002 and 2004 this resulted in total breeding failure for the 125 000 pairs of Brown Noddies breeding on Pelsaert Island. In contrast, the residential Lesser Noddy still had a breeding success of 19.6 % (1997), 10.8 % (2002) and 5.0 % (2004) during these reproductively poor years.

Discussion

The gradual delay in the onset of breeding over successive years until 1997, and reduced breeding success, indicated that some outside influence was having a negative impact upon reproductive performance of the two noddy species at the Houtman Abrolhos. The breeding success of the noddies at the

Table 2

The breakdown of timing, performance and diet for those years with sufficient data for each species studied on Pelsaert Island, Houtman Abrolhos. Years were pooled into reproductively bad or good years to illustrate the other breeding characteristics for each species in those years. We assigned seasons as "bad" when breeding success was less than 15%.

Species	Measure	Bad Seasons	Good Seasons
Lesser Noddy	Participation (%)	30.3	52.1
	First Egg Date (Day)	306	255
	Mean Lay Date (Day)	318	284
	Breeding Success (%)	9.6	40.2
	Beaked Salmon (% volume)	34.7	53.9
	Black-spotted goatfish (% volume)	46.5	20.4
Brown Noddy	Participation (%)	16.2	66.1
	First Egg Date (Day)	319	266
	Mean Lay Date (Day)	344	275
	Breeding Success (%)	0.0	18.0
	Beaked Salmon (% volume)	48.0	73.2
	Black-spotted goatfish (% volume)	2.9	0.9
N		4	7

Abrolhos appeared to be linked to the availability of large volumes of Beaked Salmon during the early (September–October) portion of the breeding season (Surman 1997; Surman & Wooller 2003; Gaughan *et al.* 2002). Overall, Beaked Salmon comprised 73 % of the diet in good years, but 48 % in bad years, although the poorer years were skewed by the appearance of Beaked Salmon in the regurgitates of Brown Noddies later in the year than would normally be expected. Crawford & Dyer (1995) observed changes in the numbers of breeding attempts, and the numbers of chicks that were raised, of four seabird species in relation to changes in the abundance of the Cape Anchovy *Engraulis capensis* in their diet. Similarly, Ramos (2000) observed a reduction in the volume of the principal prey, goatfish, in the diet of Roseate Terns breeding in the western Indian Ocean during reproductively poor years. Interestingly, at this eastern Indian Ocean breeding site, in reproductively poor years there was higher volumes of goatfish in regurgitates of both the Lesser Noddy and Brown Noddy, perhaps supplementing the decline in the presence of Beaked Salmon.

During ENSO years, reduced marine productivity may impact upon noddies at the Houtman Abrolhos through a reduction in the abundance and availability of a critical prey, the Beaked Salmon. Other major dietary components followed similar trends whether it was a good or poor year, although the proportion of Black-spotted Goatfish was higher in poorer years (Table 2). During 'poor' years the regurgitates of Brown Noddies and Lesser Noddies contained 2.9% and 46.5% Black-spotted Goatfish respectively. In contrast, during the 'good' years this percentage fell to 0.9% in Brown Noddies and 20.4% for Lesser Noddies. Lesser Noddies appeared to be better able to substitute Beaked Salmon with Black-spotted Goatfish during 'poor' years, and this may have buffered them from the severe effects of ENSO events exhibited by the Brown Noddy. The Brown Noddies inability to switch prey was likely linked to body size, foraging techniques and foraging grounds. Lesser Noddies are hoverers, dipping for minute prey just from the surface, and they consume prey of an average length of 33.5mm (N=16 559, see Surman & Wooller 2003). Brown Noddies, on the other hand, consumed prey of an average 51.3 mm (N=8 291). The small size of the larval Black-spotted goatfish (<35mm SL) may make them difficult to handle or catch for the larger Brown Noddy.

It appeared that the breeding success of the noddies at the Abrolhos was linked to the availability of large volumes of Beaked Salmon during the early (September–October) portion of the breeding season. For Brown Noddies the population suffered a complete reproductive failure in those years when the proportion of Beaked Salmon fell below 50 % by volume, and those years coincided with negative SOI values (ENSO years). Importantly, Beaked Salmon appeared to be a requirement at high volumes in the diet of Brown Noddies during the pre-laying period of the season in September/October. Overall, Beaked Salmon comprised 90% of the diet in good years, but 70% in bad years, although the poorer years were skewed by the appearance of Beaked Salmon in the regurgitates of Brown Noddies later in the year than would normally be expected. The breeding success of other seabird species have similarly been linked to prey availability at critical periods during the breeding season. For example, breeding success of kittiwake *Rissa tridactyla* colonies in the NE Atlantic have been linked to the availability and quality of their main prey, sandeels *Ammodytes marinus*, during the breeding season (Lewis *et al.* 2001; Rindorf *et al.* 2000). Crawford & Dyer (1995) also observed changes in the performance of seabirds in relation to changes in the abundance of the Cape Anchovy *Engraulis capensis*. They found the effects of the abundance of anchovies influenced the numbers of breeding attempts, the occurrence of anchovies in the diet and the numbers of chicks that were raised by four seabird species heavily dependent upon this prey.

The strength of flow of the Leeuwin Current appeared to influence the timing of delivery of Beaked Salmon larvae (sub 75mm SL) to within the foraging ranges of the noddy species at the Houtman Abrolhos. Beaked Salmon are a benthic species found in south-western waters (Hutchins & Swainston 1986), and the availability of its larvae appeared to be greater when the Leeuwin current was stronger – during non-ENSO years. This cause and effect is counter-intuitive, as the larvae are being delivered northwards against a stronger flowing southwards current. Associated with the Leeuwin Current are the northward flowing Leeuwin Undercurrent at the sub-surface, and the northward flowing Capes Current on the continental shelf during the summer months (Pattiaratchi 2005). Mixing of the Leeuwin Current and Capes Current at the Geelvink Channel may facilitate the delivery of Beaked Salmon larvae within range of the two species south and west of the Abrolhos where foraging "hotspots" of noddies occur (Surman & Wooller 2003). Since the ENSO weakens the potential for upwelling in the area, it may also affect the distribution of Beaked Salmon larvae. The Capes Current flows most strongly between October and February principally along inshore shelf waters of Western Australia, at a time that the Leeuwin Current flows most weakly. The long (3 month) larval duration of Beaked Salmon may allow their northward delivery via the Capes Current.

The precise role of the Leeuwin Current upon the diet and performance of the two noddies at the Houtman Abrolhos remains unclear. Whilst the Leeuwin Current has likely facilitated the colonisation of the Houtman Abrolhos by tropical seabirds, the dynamics of how the current delivers prey and suppresses/enhances the arrival of prey from southern regions is unknown. However, ENSO events impact severely upon the timing of breeding, the numbers of participants and ultimately the reproductive output of the two noddy species. It was evident that during poorer years, Beaked Salmon were less abundant in regurgitates of the noddies, and presumably less available within the foraging range of these species. Foraging areas of the two noddies occur south and west of the islands, at least to the shelf edge (Surman & Wooller 2003), however they are rarely observed foraging in the Geelvink Channel (Surman pers. obs.). It may be that the orientation of eddies regularly observed west of the Houtman Abrolhos may play a role in defining the distribution of Beaked Salmon larvae during ENSO years.

It would appear from the long-term data presented in this paper that the timing of breeding of Lesser and Brown Noddies is undergoing a gradual seasonal shift, more frequently commencing later in the year with an associated decrease in reproductive success. From the dietary data presented it can be surmised that this shift is likely caused by oceanographic driven changes in productivity in the waters adjacent to the Houtman Abrolhos. The noddy species will need to adapt to shifting levels of prey availability, coupled with the expected effects of increasing sealevels upon these low-lying island habitats. The long-term implications of this shift for the noddy populations, and most likely other core breeding populations of seabirds at the Houtman Abrolhos, are potentially severe.

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Current measurements at a year-long continental shelf mooring near Perth, Western Australia

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Abstract

An acoustic Doppler current profiler moored near the bottom at the 71 m isobath on the outer continental shelf 50 km northwest of Perth recorded currents at 13 levels between mid-November 2000 and late November2001. The main features were the poleward Leeuwin Current, which was strongest in winter with a maximum speed of ~0.6 ms^{-1}, and the wind-driven, equatorward Capes Current in summer with a maximum speed of ~0.9 ms^{-1}. The currents varied continuously, occasionally reversing, due to wind forcing and sometimes due to features off the shelf. Averaged over a month the Leeuwin Current was strongest nearest the bottom and it was directed off the shelf by almost 45°. Independently, there were intervals of several days when the instrument revealed that the equivalent of several tens of km of flow had passed it in a cross-shelf direction. The sea-land breeze cycle generated baroclinic inertial waves with the associated shallow and deep flows being out of phase. These flows moved water across the shelf by several kilometres. There was also a wave like phenomenon with a time scale of 15–45 hours that produced loops in the flow that were as much as 10 km across. When the Leeuwin Current was strong these loops were stretched into cusps.

Keywords: Leeuwin Current, current movements, current variability, continental shelf flows, seasonal variability, wind stress.

Introduction

The continental shelf waters north and south of Perth, Western Australia (Figure 1) are influenced by, *inter alia*, the southward-flowing Leeuwin Current (LC) that is strongest above the upper continental slope, by the northward-flowing Capes Current (CC) driven by summer southerly winds, and by passing weather systems (Cresswell *et al.* 1989; Mills *et al.* 1996; Pearce & Pattiaratchi 1999; Gersbach *et al.* 1999). The rapidly growing population of the coastal region has meant a growth of shipping, naval activities, professional and recreational fishing, coastal developments, tourism, waste management, *etc.*, There have been, however, very few long-term moored current measurements.

CSIRO had a succession of month-long deployments of single current meters 10 m above the bottom for depths of ~40–60 m south of the Abrolhos Islands over two years in the mid-1970s and near Rottnest Island for several months in that period (Cresswell *et al.* 1989). Steedman & Associates (1981) reported on current measurements that were related to the proposed Point Peron sewage disposal site and Pearce & Pattiaratchi (1999) presented plots of these. The Leeuwin Current Interdisciplinary Experiment (LUCIE) included an extensive array of moorings from NW Cape southward and then eastward to Cliffy Head (Boland *et al.* 1988; Smith *et al.* 1991). The depths at the mooring sites ranged from mid-shelf (roughly 50 m), to the shelf edge (roughly 100 m), and out to 700 m on the continental slope. The moorings comprised up to four current meters and data were collected from September 1986 to August 1987. The D2 site at the 108 m isobath at 29°33′S out from Dongara obtained an excellent set of records from four depths. The Perth Coastal Waters Study (PCWS) maintained current meters at mid depth at the 200 m, 110 m and 27 m isobaths at intervals during 1992 to 1994 (Lord & Hillman 1995) and Pearce *et al.* (2006) presented the mean monthly north-south current components for these. There was a short (two-week) mooring deployment in the Sepia Depression near Point Peron by Mills *et al.* (1996). From June 2004 to July 2005 three moorings were maintained at the 100 m, 40 m and 20 m isobaths along a line out from Two Rocks at 31°30′S north of Perth. The instruments were rotated every three months and included ADCPs, CTDs and bottom-mounted pressure gauges. Preliminary findings appear in Fandry *et al.* (2006).

Most of the continental shelf current meter records showed the northward-flowing CC in summer and the southward-flowing LC in winter. The Abrolhos and Rottnest current meters revealed current reversals related to forcing by weather systems throughout the year. In *summer*, strong southeasterly wind events on the western sides of atmospheric highs passing from west to east drove northward current pulses of up to 0.4 ms^{-1} and lowered coastal sea level by about 0.3 m. Between these events atmospheric lows reduced the southeasterly winds and there was southward current of about 0.1 ms^{-1}. In *winter* northwesterly storms from passing lows drove southward current pulses of as much as 0.6 ms^{-1} and raised coastal sea level by up to 0.8 m. Northward flow sometimes occurred at times between these events. Not all current events could be related to weather forcing and some may have been due to the incursions of mesoscale features of the LC.

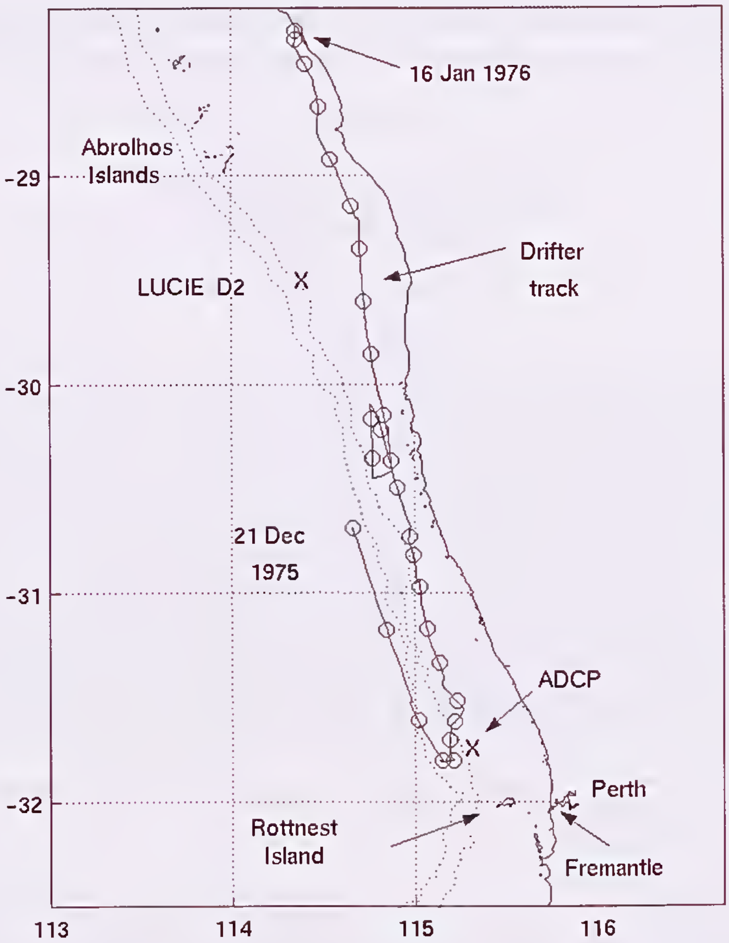


Figure 1. The location of the ADCP mooring, the Lucie D2 mooring, and the track of a drifter showing daily positions showing both the southward Leeuwin Current off the continental shelf and the northward Capes Current on the shelf. The 100 and 200 m isobaths are marked with dotted lines.

The important role of weather systems in winter was also reported by Mills *et al.* (1996): in one case southward and onshore wind stress moved buoyant LC water shoreward, while at the same time there was an offshore flow near the bottom. In another case, the winds were weak and an anticyclonic meander of the LC drove northward flow over the shelf. However, steeply-inclined isopycnals at the mid-shelf opposed any cross-shelf exchange of water.

The seasonal current pattern due to the Leeuwin and Capes Currents is also evident in satellite imagery (Pearce & Pattiaratchi 1999), as well as in Lagrangian data, such as the drift card releases of Rochford (1969) and the satellite tracked drifters of Cresswell & Golding (1980): a drifter in summer interchanged between the southward LC moving at ~0.7 ms^{-1} above the upper continental shelf and the northward CC flow moving at ~0.2 ms^{-1} on the outer shelf (Figure 1). The drifters on the shelf reversed their northward flow as weather systems passed over (Cresswell *et al.* 1989).

Monthly time series data from a transect off Hillarys 20 km north of Perth showed that the cross-shelf exchange, which has important marine ecological implications, is affected by three dominant mechanisms: mesoscale meanders of the LC, smaller-scale tongues of LC water penetrating across the continental shelf, and high density nearshore waters episodically cascading offshore down the seabed (Pearce *et al.* 2006).

In this paper, in order to examine some of the phenomena identified above, we discuss hourly data from an Acoustic Doppler Current Profiler, ADCP, that was moored for a little over a year a few metres above the bottom at the 71 m isobath out from the northern suburbs of Perth (Figure 1). Unlike current meters at discrete depths, the ADCP collected data from 4 m-thick bins up through the water column, albeit losing the top 15% because of side lobes from the ADCP transducers. The ADCP was put at this location so that it would come under the influence of both the CC in the summer and perhaps incursions by the LC in all seasons. The record shows both these currents and it is rich with the effects of other phenomena including flows off and onto the continental shelf, sea/land breezes, summer and winter storms, and wave-like perturbations with periods up to several days. We complement the ADCP data with wind and sea level data.

Methods

The ADCP was housed within a syntactic foam float and moored 3 m above the bottom at the 71 m isobath for a total of 54 weeks. The attachment to the anchor was via two acoustic releases mounted in parallel. When our technicians returned to mooring after one year neither of the releases functioned. Three more days were spent over two weeks working with highly skilled divers from the Perth Diving Academy who eventually recovered the instrument. Both releases were heavily encrusted with corals. The mooring and the instrument were serviced and redeployed and recovered after another year. The instrument did not work on the second deployment. The ocean does not willingly volunteer its secrets.

With the present data set the centre of the first 4 m-thick ADCP bin was at 65 m. Hourly data were acquired up through the water to bin 13 at 17 m depth. Shallower than this, side lobes from the instrument's four acoustic beams, each directed 30°C away from the vertical, introduced noise and the data from those bins had to be ignored. The Doppler shifts of the returned signals for bins 1–13 were processed with the manufacturer's software and yielded profiles of current speed and direction. The instrument recorded temperature. The current data from the ADCP were resolved into cross-shelf and along-shelf components – the shelf edge is aligned roughly 27° west of north. On-shelf flow (positive) is to the ENE and off-shelf flow (negative) is to the WSW. The along-shelf components are NNW (positive) and SSE (negative).

A simple calculation of wind stress was made from the hourly meteorological data collected by the Bureau of Meteorology at Rottnest Island, namely $1.2 \times 0.0013 \times s^2$ Nm^{-2}, where s is the wind speed. The stress was resolved in north-south and east-west components, as much of the forcing was north-south.

Hourly sea level measurements from Fremantle were adjusted for the inverse barometer effect at 0.01 m per hPa from an arbitrary baseline of 1020 hPa with the Rottnest Island atmospheric pressure measurements.

Results

Annual signal

The along and cross-shelf current-depth-time plots (Figure 2A, B) hint at the complexity of the water movements on the shelf, as does the time series of sea level at Fremantle, wind stress at Rottnest Island, and

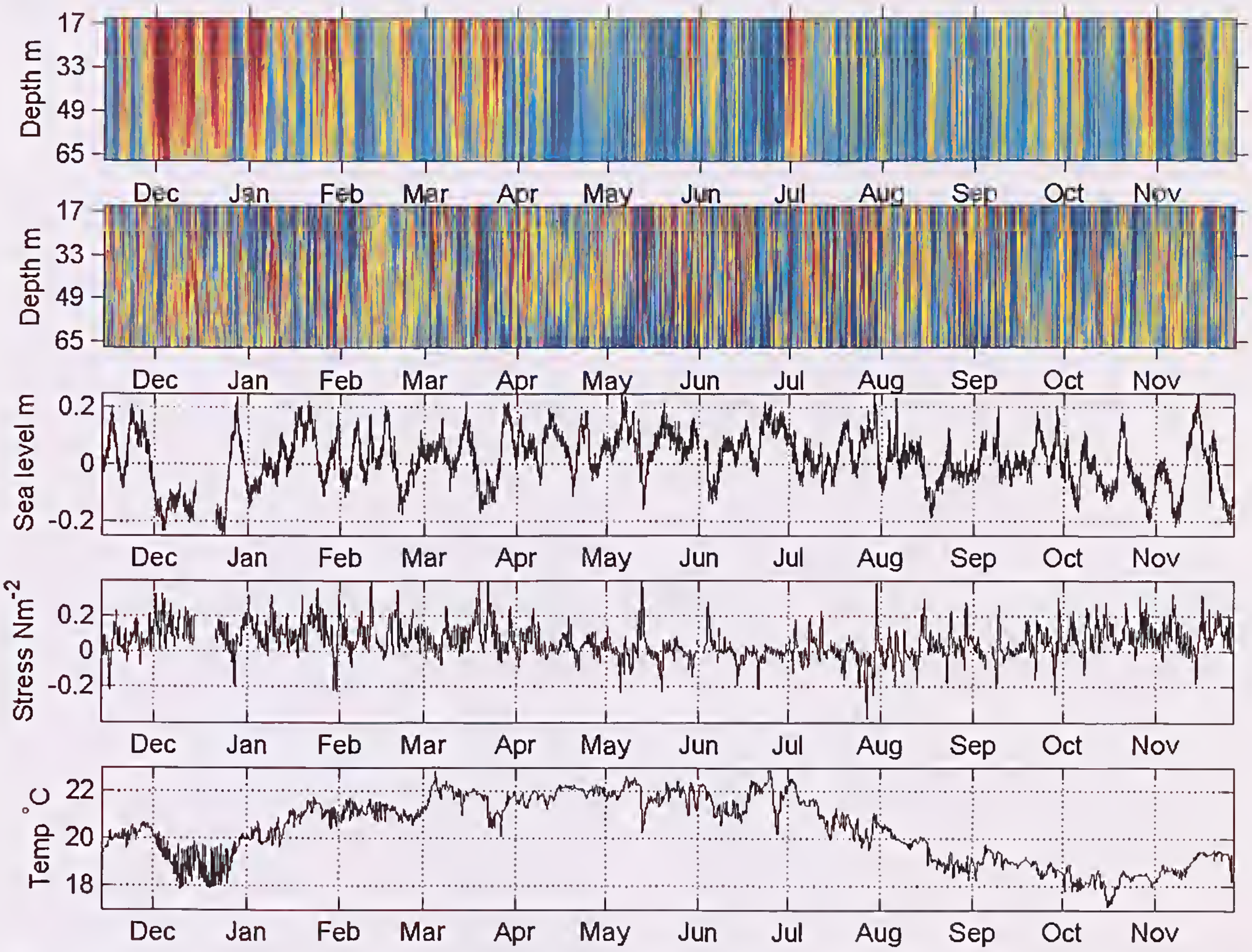


Figure 2. A) The along-shelf and B) the cross-shelf currents measured by the ADCP and presented in a component strength-depth-time format. The scales, with the ranges (-0.4 to 0.4 and -0.15 to 0.15 ms^{-1} respectively) were chosen to emphasize the variability in the record. In A) red is along the shelf to the NNW and blue is to the SSE. In B) red is flow onto the shelf and blue is flow off. C) Adjusted sea level at Fremantle. D) The along-shelf wind stress calculated from the Rottnest Island wind measurements. E) The temperature measured at four metres above the bottom by the ADCP. The period covered is 13 November 2000 to 27 November 2001. All values are hourly, but the wind stress has been smoothed slightly (5-hour running mean).

temperature recorded at the instrument (Figure 3C–E). The along-shelf current component showed that there were intervals of LC flow (blue) at times of decreased positive wind stress and increased sea level in November 2000. For the first three weeks of December 2000 the winds of temperate WA were controlled by a large high (>1020 hPa) centred near 90°E, more than 2000 km west of Perth. This drove northward wind stress greater than 0.1 Nm^{-2}, and up to 0.3 Nm^{-2}, a strong CC (red in Figure 2A), and low sea level. The mooring experienced low temperatures with a daily variability of more than 1°C that was related to cycles of the sea and land breezes – to be discussed later. The CC had a peak speed of 0.9 ms^{-1}.

From January through late March there were intervals of positive and negative along-shelf flow and then the LC arrived and drove predominantly ESE (blue) flow through to near the end of the record. Sea level became positive for over four months after the arrival of the LC and the wind stress tended towards zero, only becoming northward again, with low sea level, in October. One might have expected the LC to cease then, but this was not the case. The LC held the temperature at the ADCP above 21°C from early March until early July – in other words, contrary to the normal seasonal signal because of the supply of warm tropical waters. In late June the flow reversed for ten days (red) and reached surface speeds of 0.4 ms^{-1}. The LC had been quite strong immediately prior to this, reaching speeds of 0.6 ms^{-1}. There were many other shorter intervals of WNW (reverse) flow while the LC was flowing. The cross-shelf flow showed similar variability, together with vertical shear, such that on-shelf flow (red) occurred at mid-depth in December and off-shelf flow (blue) occurred in the lower water in the winter months April to August. The lowest temperature of 17.1°C occurred in October.

The monthly progressive vector diagrams (PVDs) for three selected depths: 17 m; 41 m; and 65 m, reveal a little more about the currents (Figure 3). If the ocean was infinite with unchanging bottom topography where individual depth strata moved as if they were solid, then PVDs would show the trajectories of particles from the mooring site. At the continental shelf mooring site the situation is, obviously, more complex, with shoaling to the east and deepening to the west, where the LC is found. Even so, we suggest that PVDs serve as "signatures" of behaviour that are sometimes more readily recognizable than in time series.

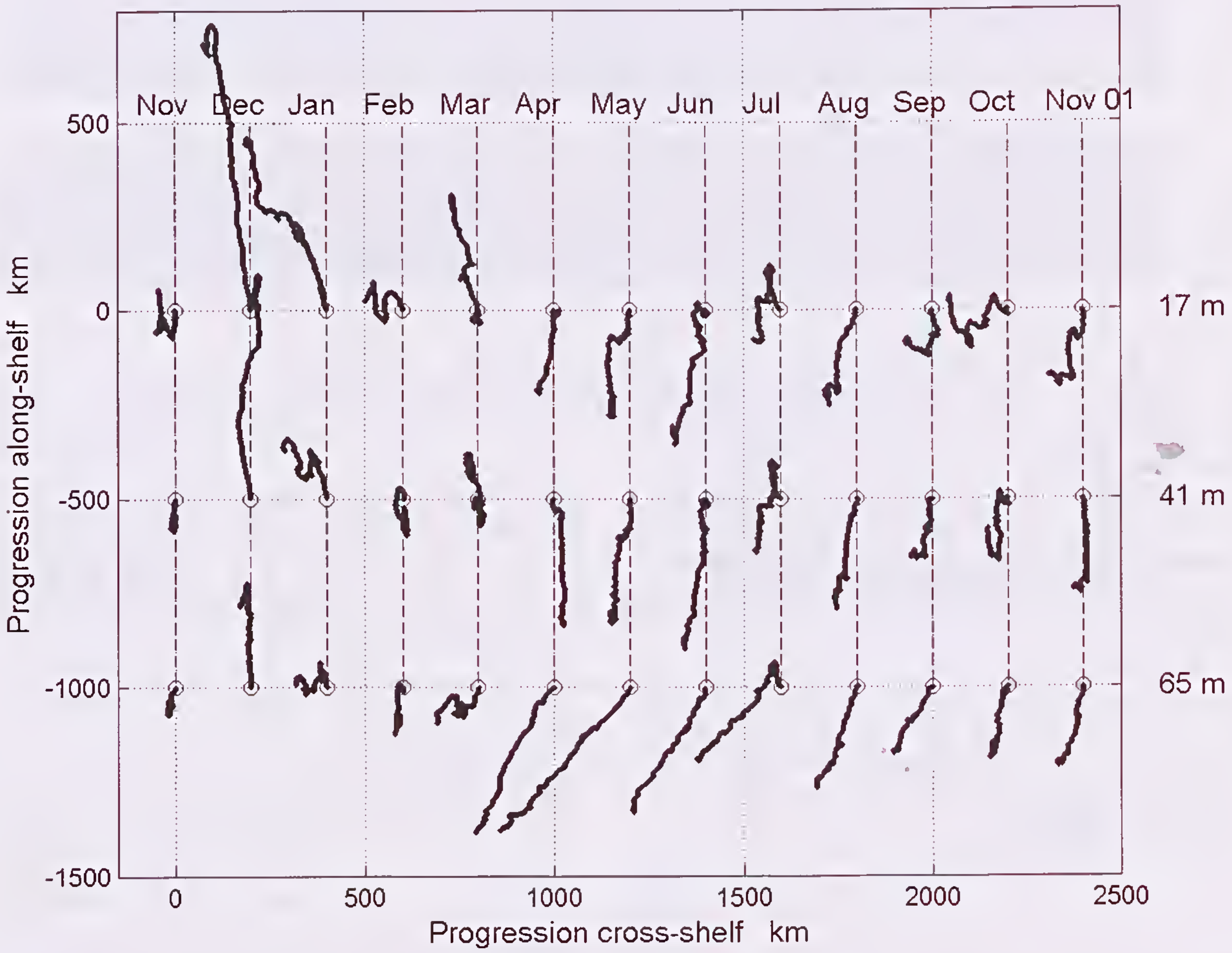


Figure 3. Monthly progressive vector diagrams (PVDs) for water depths 17 m (bin 13), 41 m (bin 7) and 65 m (bin 1). The PVDs are arranged by row for the different depths, and by column for the months, with successive months being offset by 200 km. The November 2000 PVD is short because the record started on 13 November. The November 2001 PVD only extends to 26 November, when the instrument was recovered. The axes are across and along the bottom topography.

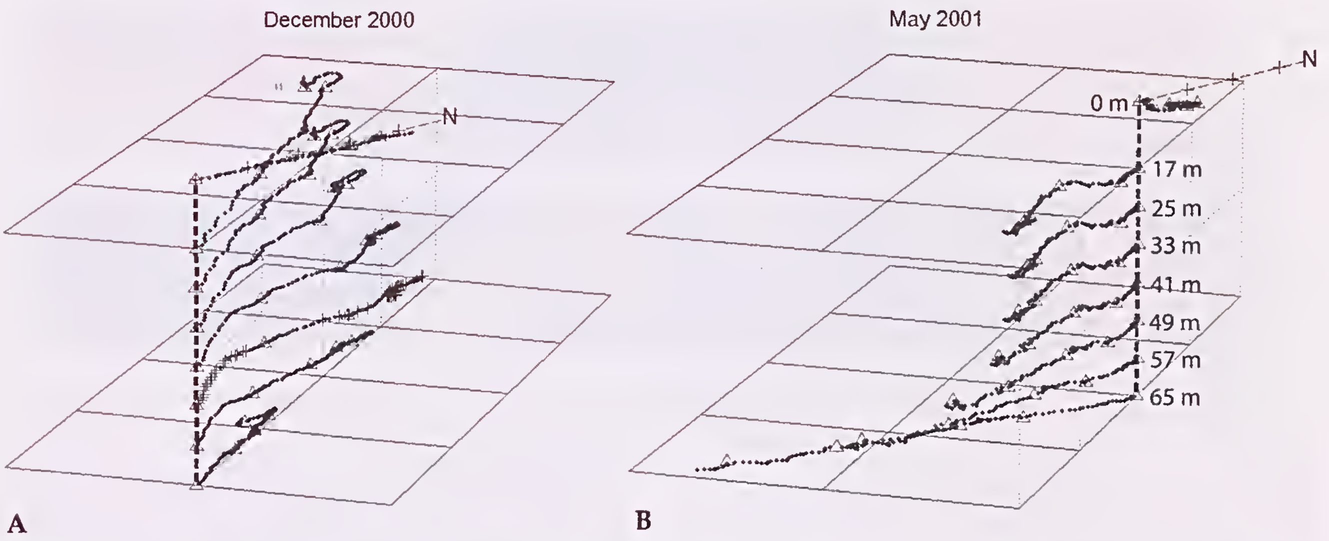


Figure 4A. Progressive vector diagrams plotted six-hourly for the wind stress (top) and every second ADCP bin (depths 17, 25,...65 m; dots) for December 2000 when the CC was strongest. All the motions are horizontal. The triangles mark successive weeks of progression. The pluses on the PVD for 49 m depth (bin 5) indicate when the temperature measured by the ADCP exceeded 19.2°C. The horizontal meshes are made up of 200 km squares with the upper one being at 17 m depth and the lower one at 65 m depth. The vertical grid (dotted) is aligned parallel with the shelf edge. The top of the thick vertical dashed line is the sea surface and the angled dashed line from there towards the upper right indicates north, with the plus signs being a scale showing the wind stress progression at 0.1 Nm^{-2} for one week. The view is out across the shelf towards the northwest.
Figure 4B. As for Figure 4A, but for May 2001 when the LC was strongest.

The wind-driven CC in December was strongest at the uppermost bin at 17 m depth, with an overall apparent drift component along the shelf of 700 km, equivalent to a mean speed of 0.25 ms^{-1}. The waters moved off-shelf by 100 km during the month. The current was also quite strong at mid-depth, with an on-shelf component in the second half of the month. The CC was present, but weaker, in January and March, again with components of off-shelf flow. At 65 m shows in March the flow had components both off-shelf and poleward, the flow direction of the LC. Late March appears to have been the onset of the LC that continued throughout the record and was generally strongest near the bottom, usually with a strong off-shelf component. The LC flow near the bottom reached a maximum in May with over 500 km of water going past the mooring with an along-shelf component of -0.14 ms^{-1} and a cross-shelf component of -0.12 ms^{-1}. The surface flow of the LC was weaker, perhaps due to those waters being more susceptible to northward wind forcing from passing storms, and it was more aligned with the shelf. The 10-day pulse of reverse flow that was seen in the time series can be seen in the upper two PVDs at the end of June/start of July.

A perspective 3D view of the PVDs for December 2000 (Figure 4A) when the along-shelf CC was at its peak strength showed on-shelf flow at mid-depths, but not near the bottom, in the middle two weeks of the month. The on-shelf flow coincided with temperatures at the ADCP decreasing by 2°C, albeit with daily oscillations for much of the month (Figure 2), so possibly this was due to intrusions of cold continental slope water that was associated with the strong CC. It is puzzling that the flow at 65 m – closest to the ADCP and its temperature sensor – did not register an on-shelf component. The on-shelf flow was strongest at bin 5 (49 m) and it corresponded with low temperatures being measured at the ADCP: the PVD is marked by dots rather than plus signs. The wind stress PVD for the month was strongly northward apparently averaging more than 0.1 Nm^{-2}, but note that eight days were missing from the Rottnest wind data, so it would have been stronger than shown.

A similar perspective view of the PVDs for May 2001 (Figure 4B) when the LC was strongest showed a smooth transition from the mainly along-shelf (SSE) flow near the surface that progressively turns off-shelf and increases in strength with depth. As compared with December, the wind stress PVD was small.

Two significant current reversals

Leeuwin Current in summer 2000/2001

Two instances of summer flows of the LC in November 2000 have already been mentioned. Here we discuss an interval in late December 2000 (Figure 5) when the wind stress, which had reached 0.3 Nm^{-2} earlier in the month under the influence of a 1020+ hPa high at about 90°E, decreased to less than 0.1 Nm^{-2} northward and reversed to 0.2 Nm^{-2} southward on 27/28 December. The interruption to the northward wind flow from the high near 90°E came from the combined effects of a small 1004 hPa low over Perth and a 1024 hPa high centred south of the Great Australian Bight at 40°S, 130°E. During this time the current ran southward as a LC, peaking at 0.4 ms^{-1}, and sea level rose (as is the case when the LC flows), by 0.4 m. The current reversal commenced with off-shelf flow of 0.1 ms^{-1}, but this was somewhat masked in the time series in Figure 5 by a daily oscillation of amplitude as much as 0.15 ms^{-1}.

Perspective views of PVDs covering respectively four days from prior to the event to its peak, and four days from the peak until after the event appear in Figure 6A, B. The first, 24–27 December, shows how particles that

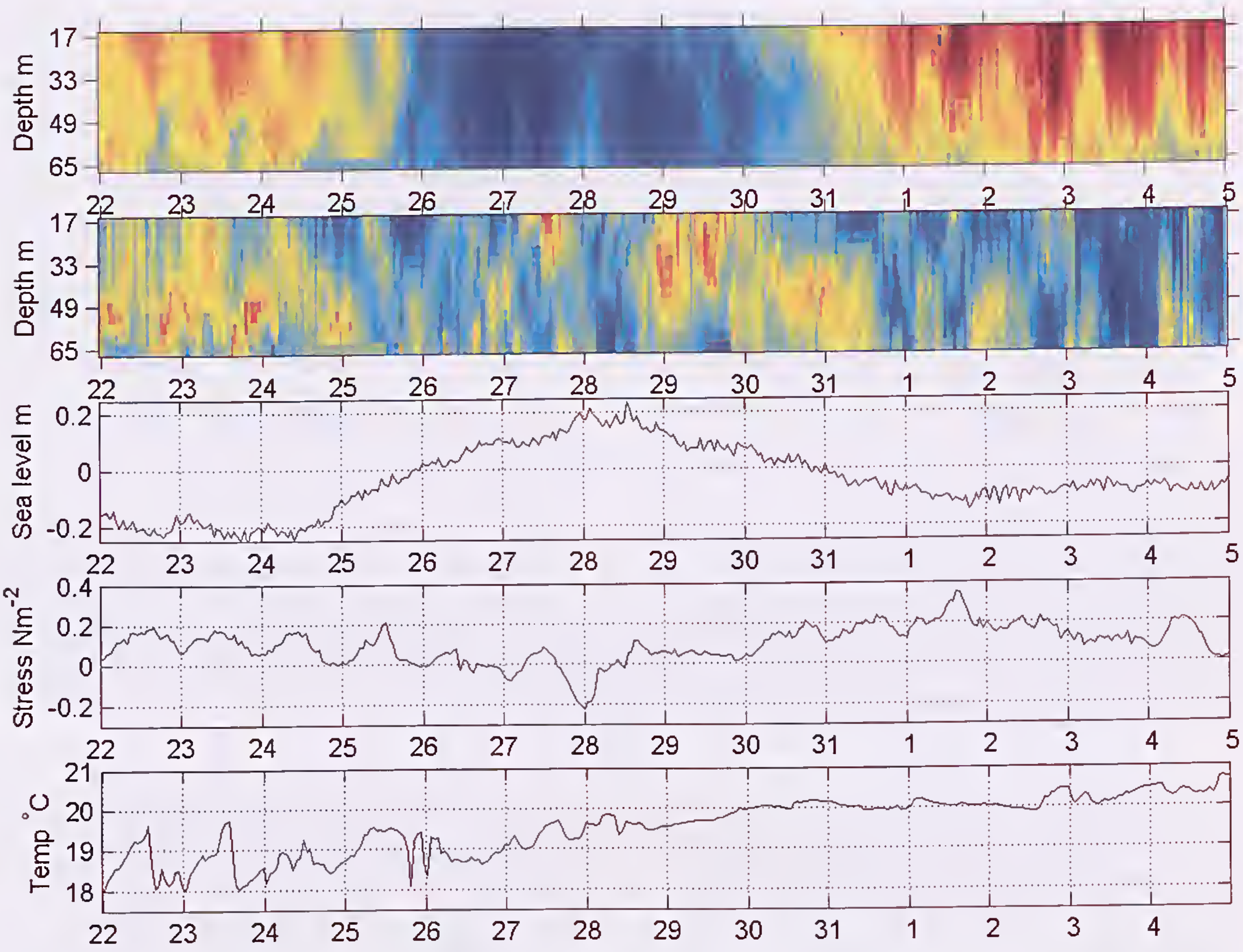
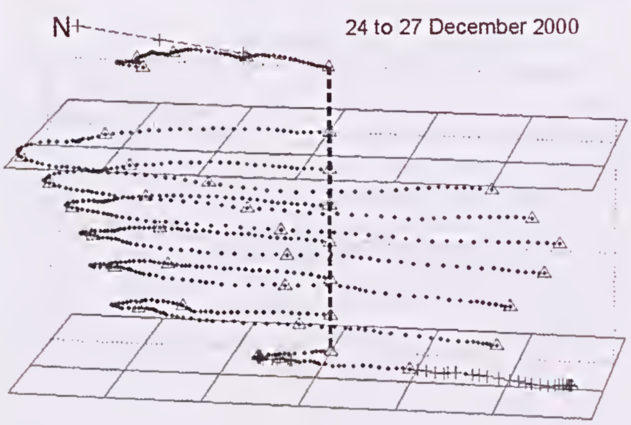


Figure 5. As for Figure 2, but from 22 December 2000 to 5 January 2001 with the ranges for A and B as -0.35 to 0.5 and -0.25 to 0.25 ms^{-1} respectively.



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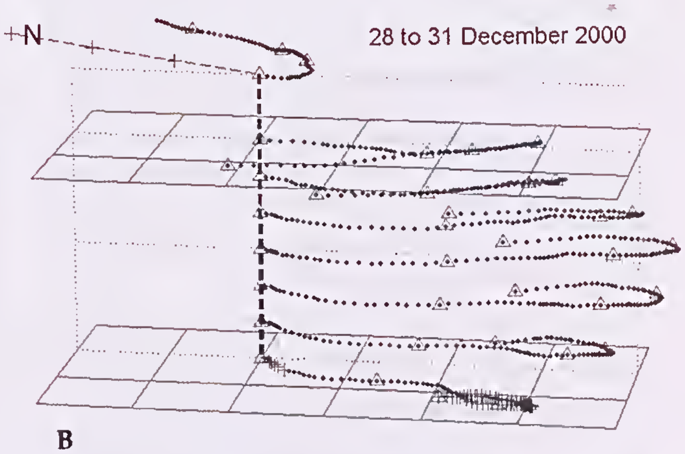


B

Figure 6A. Progressive vector diagrams plotted hourly for the wind stress (top) and every second ADCP bin (depths 17, 25,...65 m) for UTC 24 to 27 December 2000inclusive. All the motions are horizontal. The horizontal meshes are made up of 10 km squares with the upper one being at 17 m depth and the lower one at 65 m depth. The vertical grid(dotted) is aligned parallel with the shelf edge. The top of the thick vertical dashed line is the sea surface and the angled dashed line from there indicates north. The '+' signs along it are a scale for the wind stress, showing the progressions that would be made in 24 hours at 0.1, 0.2 and 0.3 Nm^{-2}. The pluses on the 65 m depth PVD indicate when the temperature exceeded 19°C. The triangles on all PVDs are one day apart.

Figure 6B. As for Figure 6A, but for UTC 28 to 31 December 2000 inclusive, with the pluses on the 65 m PVD being for temperatures greater than 19.8°C.

left the mooring under the influence of the CC turned off-shelf as the wind stress PVD weakened and were then carried in a LC. The second, 28–31 December, shows the wind stress to reverse once again and to become strongly northward. The current, however, did not reverse for two more days until the northward wind stress exceeded 0.1 Nm^{-2}. The reversal at 17 m (bin 13) preceded those at 41 and 65 m by 18 hours. A linear fit to a scatter plot of the along-shelf current at 17 m with the north-south wind stress for this interval showed that zero current occurred when the northward wind stress was ~0.06 Nm^{-2} and that when the wind stress was zero the current became southward at ~0.27 ms^{-1}.

Reversal of the Leeuwin Current in late June 2001

There was a sudden reversal of the LC in late June (Figures 7 and 8) that initiated the longest period, one week, of NNW flow between April and November, with speeds at 17 m depth reaching 0.5 ms^{-1}. Immediately prior to this the LC was unusual in that it was strongest at the surface (up to 0.5 ms^{-1}) and progressively weakened with increasing depth to 0.2 ms^{-1} at the lowest level. The weak on-shelf wind stress is unlikely to be the cause of the reversal. The temperature, which had been over 22°C, dropped 2°C prior to the reversal and then increased. Sea level fell by 0.2 m, but this occurred about 2 days after the northward current was strongese. The recovery of the LC was quite slow and faltering, taking about one week and is not treated in detail here.

What was the cause of the strengthening of the LC and then the reversal? Figure 9 shows satellite sea surface temperature images for 21, 26 and 28 June and 5 July 2001. (There were numerous cloud-free images between the first and third images, but none between the last two). The first three images showed a meander of the LC to develop into an anticyclonic eddy that moved southward above the continental slope. On 26 June the LC south of the eddy had moved eastward to be entirely on the continental shelf, thereby explaining the stronger currents detected by the ADCP. The eddy continued to move southward and then it spread across the shelf into the mooring site, which seems to explain the current reversal. From 29 June to 5 July the eddy apparently moved back to the north and the effects of the LC were then felt again at the mooring.

Cross-shelf flows both near the surface and near the bottom

28 to 30 May 2001 – off-shelf flow at depth

The wind stress was weak and variable, so it was unlikely to have been the driving force for the positive

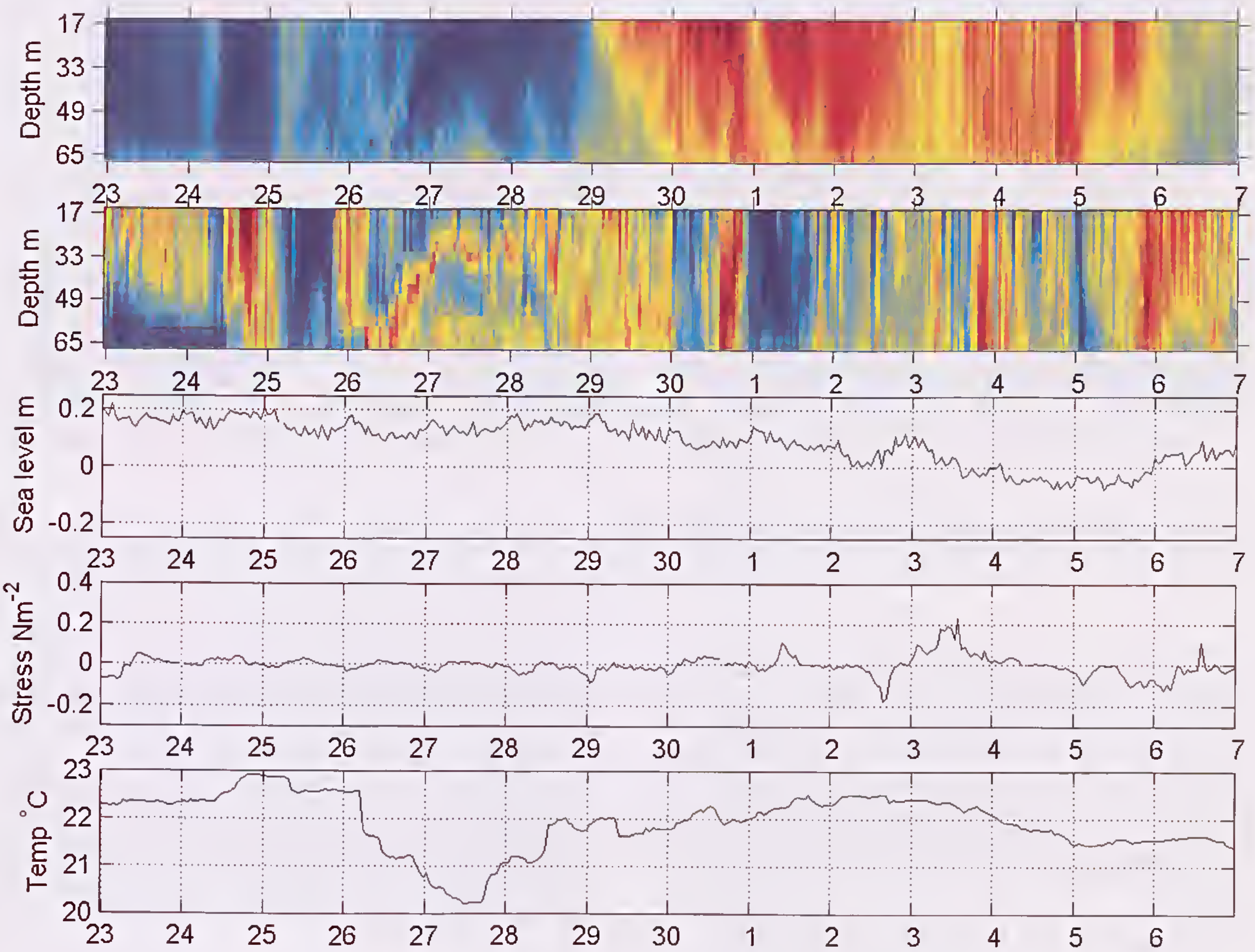


Figure 7. As for Figure 2, but for UTC 23 June to 6 July 2001 inclusive, with the ranges for A and B as -0.5 to 0.45 and -0.3 to 0.2 ms^{-1} respectively.

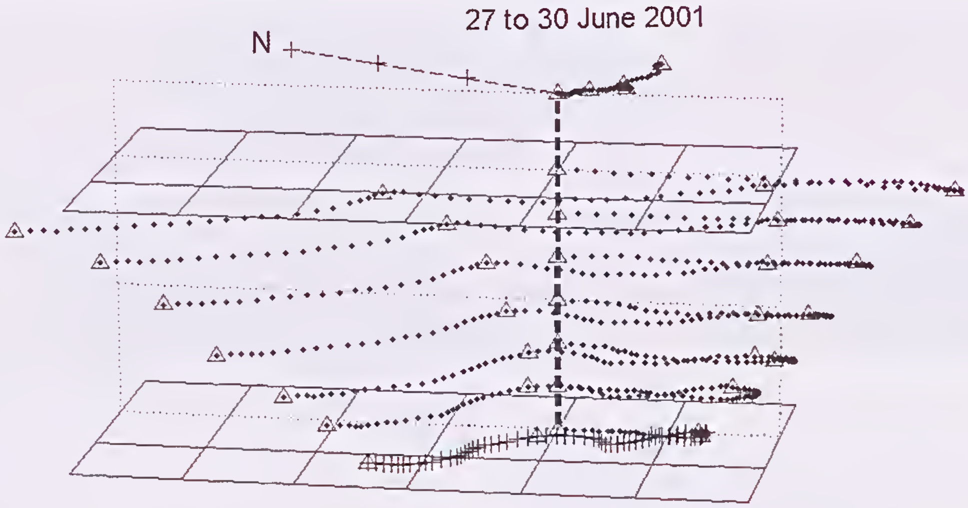
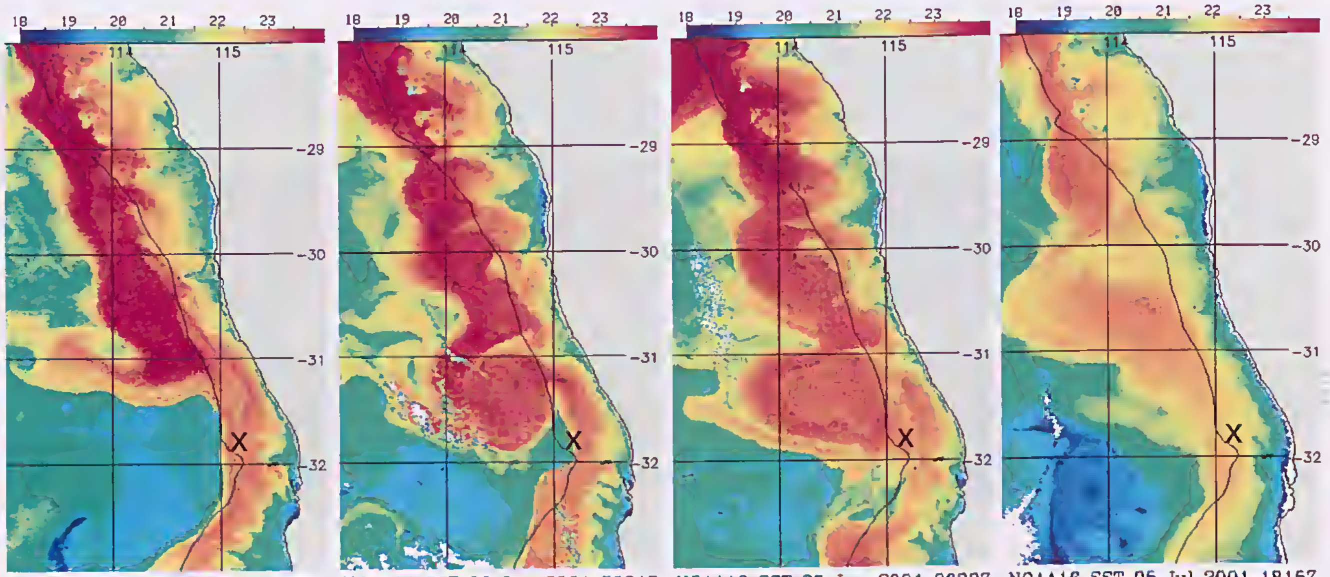


Figure 8. As for Figure 6A, but for UTC 27 June to 30 June 2001 inclusive; the pluses on the 65 m depth PVD indicate when the temperature exceeded 21.8°C.



NOAA16 SST 21 Jun 2001 0600Z
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NOAA14 SST 26 Jun 2001 2021Z
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NOAA16 SST 28 Jun 2001 0630Z
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NOAA16 SST 05 Jul 2001 1815Z
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A B C D

Figure 9. A–D: Satellite images of sea surface temperature for 21, 26 and 28 June and 5 July 2001 during which time the LC as monitored at the mooring, marked "X", initially strengthened, then reversed (due to the anticyclonic eddy seen in Figure 9C), and then recovered. The colour scale for temperature is at the top of the images and the edge of the continental shelf is marked by a thin line.

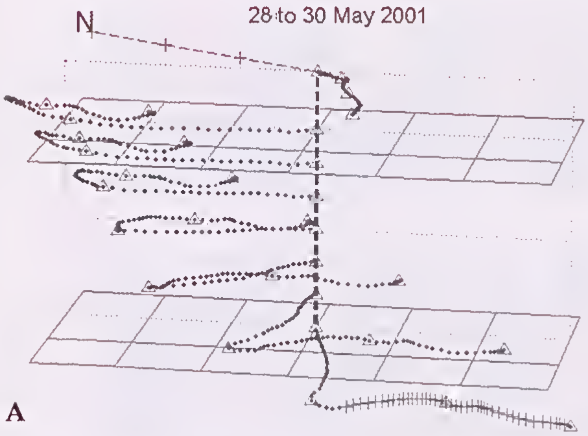
along-shelf currents that exceeded 0.3 ms^{-1} NNW in the upper part of the water column (Figure 10A). From mid-depth to the bottom there was a rotation in the flow direction, with relatively cool water flowing off-shelf at the bottom. This flow ceased with a right-angled turn to the SSE as the upper currents reversed to flow in the same direction. The temperature at the bottom increased from 21°C to 22°C in six hours, perhaps due to LC water reaching the mooring. A similar cycle of events was repeated in the next three days, but is not shown here.

14 to 18 October 2001 – off-shelf flow near the surface

The coldest water during the one-year record was recorded at this time. The wind stress showed a sea-land breeze cycle with magnitudes up to 0.2 Nm^{-2} and this had an influence on the along-shelf flow of 0.3 ms^{-1} peak-trough with a delay of about 4 hours. The flow at 17 m (top bin) was off-shelf and about 30° positive along-shelf (Figure 10B). At the mid-depths the flow was in the opposite direction. This was the case for the first day at the bottom, but the flow then turned to flow to negative along-shelf (SSE). The temperature at the ADCP was initially 18.2°C but then the on-shelf flow apparently brought colder water (17.2°C) to the ADCP over the course of one day, and then the temperature recovered two days later to 18°C.

Rotary flows

Progressive vector diagrams made from the records showed many cases of anticyclonic rotations with time



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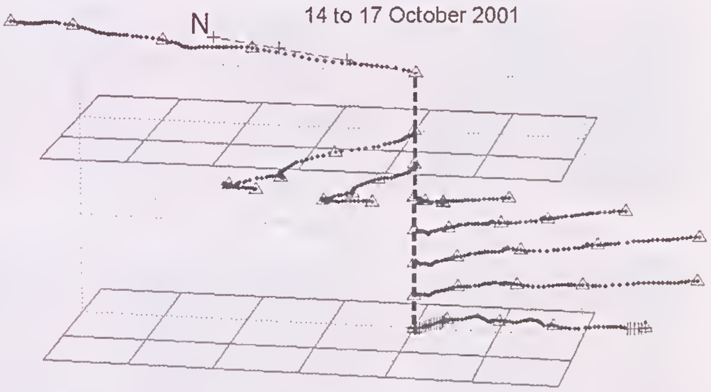

B

Figure 10A. As for Figure 6A, but for UTC 28 to 30 May 2001 inclusive, with pluses on the 65 m depth PVD indicating when the temperature exceeded 21.8°C.

Figure 10B. UTC 14 to 17 October 2001 inclusive, with pluses on the 65 m depth PVD indicating when the temperature exceeded 17.7°C.

scales from about 15–45 hours (the inertial period at the latitude of the ADCP mooring is 22.6 hours). If the LC was too strong then the loops were stretched to become cusp-like oscillations. We cannot discuss all of the cases here. Rather, we will examine six examples of several days duration. In some of the other instances the "orbits" followed by water particles at different depths were grossly complicated by strong vertical shear.

9 to 12 January 2001

The northward wind stress from a 1030 hPa high at 95°E exceeded 0.3 Nm^{-2} on the first day and this apparently drove the upper waters along the shelf to the NNW. The effect of the wind forcing rapidly decreased with depth and apparently had no effect in the lower half of the water column (Figure 11A). The alongshore current measured at 17 m lagged behind the northward wind stress by about 5 hours. The PVDs in the lower half of the water column revealed the signature of a wave that was masked or not present nearer the surface. The wave arrived at all these depths at about the same time and brought warmer water to the instrument.

12 to 14 June 2001

The wind stress was near-zero for two days before this interval and then for two days into it, so wind was unlikely to have been the trigger for any unusual water movements. The LC was strong near the bottom where it had an off-shelf component as compared with the shallower levels (Figure 11B). A significant influence came from a wave-like motion that produced anticyclonic loops through the water column; these were in phase and were described in about 30 hours at ~0.4 ms^{-1}. This was followed by an on-shelf meander at all depths. The temperature at the mooring was coldest when the flow was off-shelf, perhaps due to cool shelf waters reaching the mooring, and warmest at other times, perhaps when the edge of the LC had migrated shoreward.

19 to 21 July 2001

The wind stress was very small and unlikely to be a driving force for the currents. The current PVDs suggest that two waves passed the mooring (Figure 11C). Perhaps the LC was too strong for the anticyclonic loops to be described (the maximum speeds along the trajectories were 0.4 ms^{-1}. The cusps were separated by about 35 hours. The deep flow had a strong off-shelf component, but nearer the surface the flow was more aligned with the topography. The onshore excursions due to the waves brought slightly warmer (0.5°C) water to the mooring.

24 to 26 July 2001

The PVDs for the currents (Figure 11D) are reminiscent of those for June 12 to 15. The translation due to the LC in this case was stronger throughout the water column, possibly because winter cooling and convection led to a deep surface mixed layer. There was a current loop at most depths due to a wave and at 17 m (the uppermost bin) this was described in about 24 hours at ~0.2 ms^{-1}. Nearer the bottom the loop appeared to have been stretched into a cusp. The wind stress was southward for half a day at up to 0.2 Nm^{-2}, then it decreased to near-zero for almost a day, and finally reached 0.25 Nm^{-2} over the course of the last half day. The upper currents appeared to respond to these two intervals of strong southward wind forcing, reaching 0.3 ms^{-1}. The temperature behaviour was more complicated than in the June example.

27 to 29 July 2001

The wind stress had southward spikes of exceeding 0.4 Nm^{-2} and 0.3 Nm^{-2} around hours 12 and 60 of the 3-day interval. These were associated with atmospheric lows southwest and south of Perth respectively. Between and after these spikes the stress was near-zero. The LC was strongest near the bottom, where it flowed at an angle off the shelf (Figure 11E). At mid-depth it ran parallel to the shelf edge and nearer the surface it had a small onshore component. Three waves appear to have passed by the mooring, with the second producing anticlockwise loops in the upper part of the water column. The timings between the first and second and the second and third perturbations were about 20 hours.

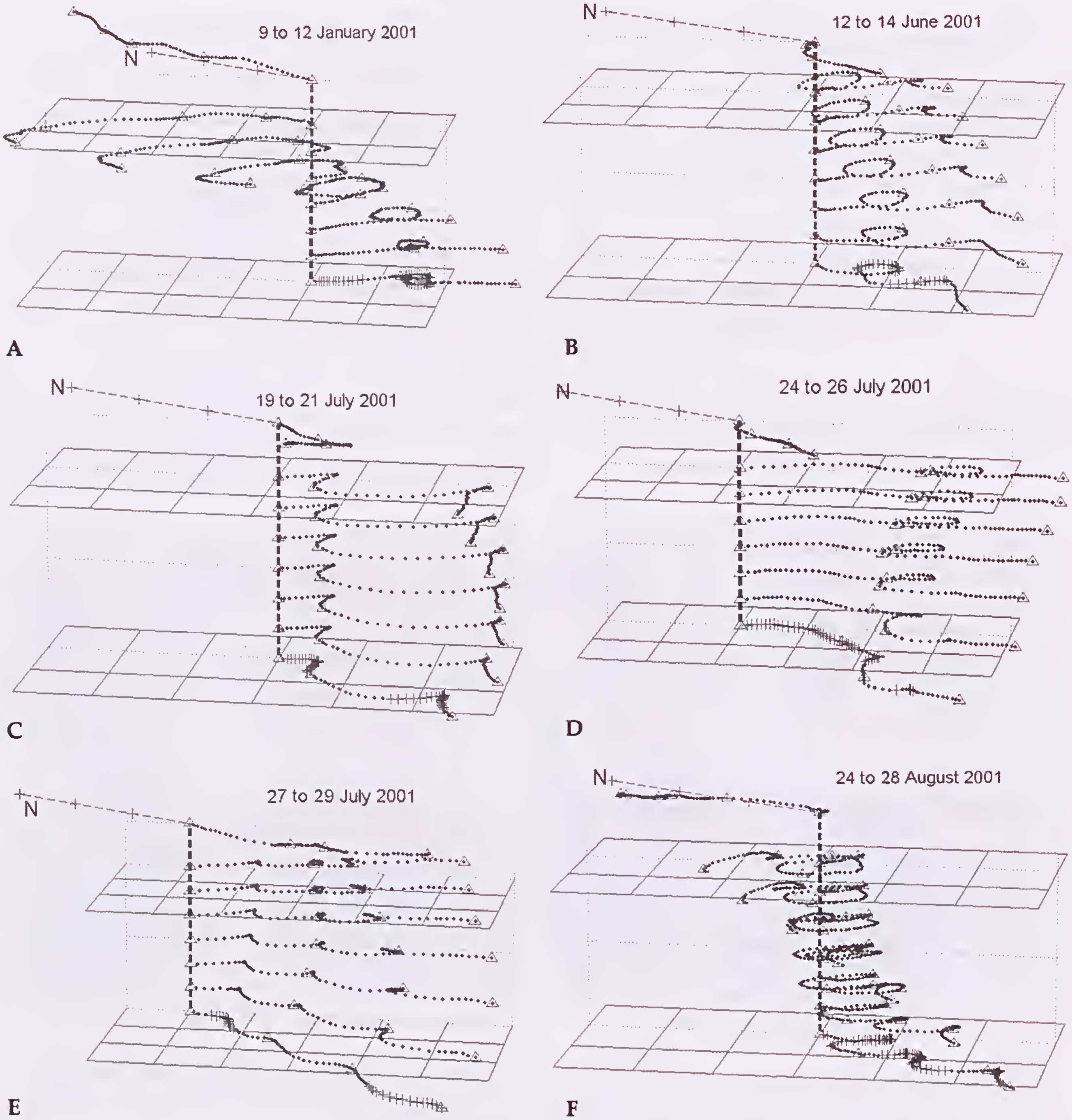

Figure 11A. As for Figure 6A, but for UTC 9 to 12 January 2001 inclusive, with pluses on the 65 m depth PVD indicating when the temperature exceeded 21.2°C; B) for UTC 12 June to 14 June 2001 inclusive, with pluses indicating when the temperature exceeded 21.2°C; C) for UTC 19 to 22 July 2001inclusive, with pluses indicating when the temperature exceeded 20.8°C; D) for UTC 24 to 26 July 2001 inclusive, with pluses indicating when the temperature exceeded 20°C; E) for UTC 27 to 29 July 2001 inclusive, with pluses indicating when the temperature exceeded 20.2°C; F) for UTC 24 to 28 August 2001 inclusive, with pluses indicating when the temperature exceeded 18.8°C.

The speeds along the trajectories ranged from 0.05 to 0.5 ms^{-1}. The temperature at the ADCP varied between 19.5°C and 20.5°C, but its variation was too slow to be related to the individual perturbations.

23 to 28 August 2001

A cold front passed over some ten hours before the interval covered for the diagram (Figure 11F) and it drove a southeastward pulse in the wind stress for about six hours that reached 0.2 Nm^{-2}. Twenty hours later a high centred at 90°E drove northward wind stress that exceeded 0.2 Nm^{-2} for half a day. After that it was near-zero. The LC was present only in the deeper part of the water column, as if the wind stress may have retarded it nearer the surface. There appeared to be no net movement at mid-depth. There were three oscillations

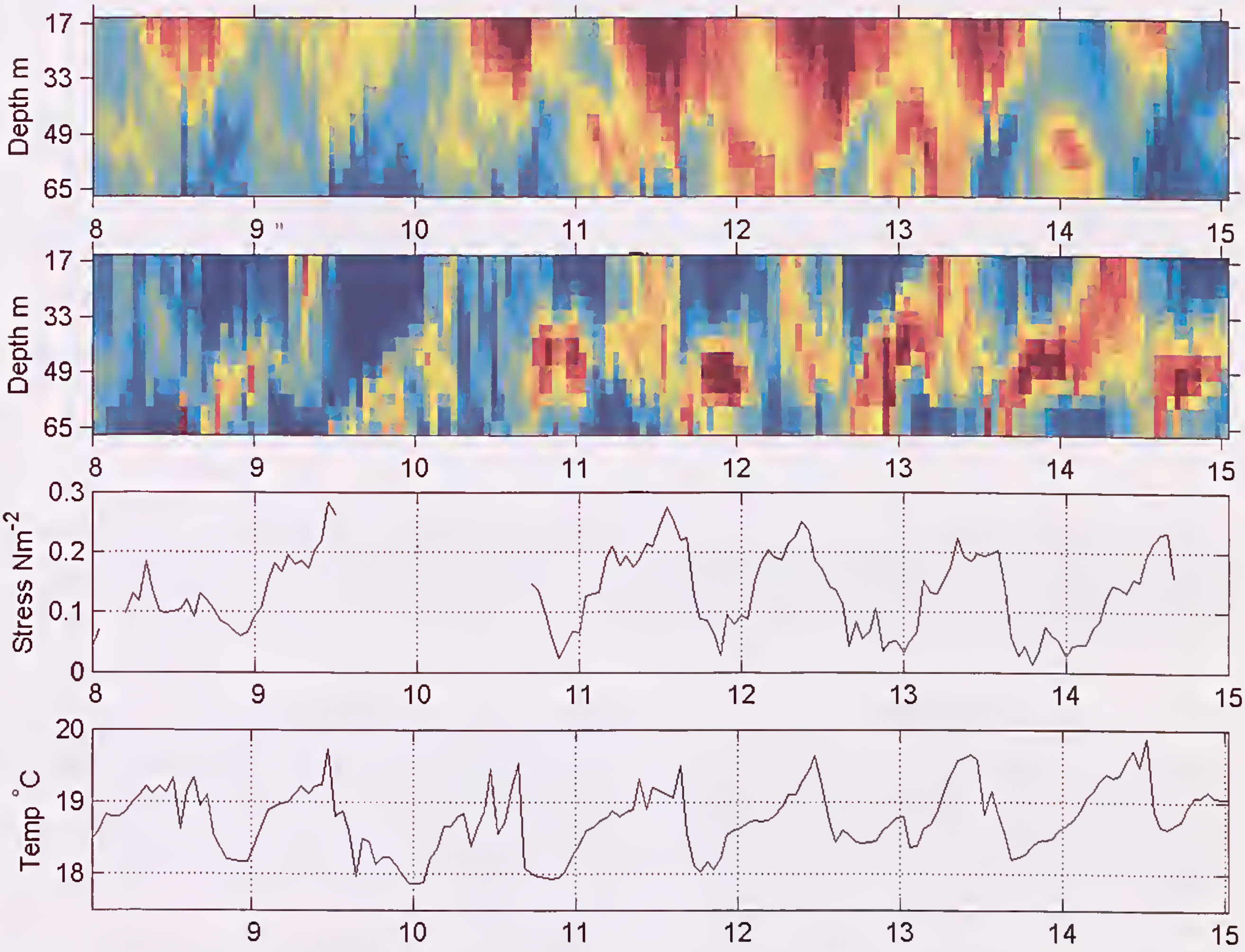

Figure 12. As for Figure 2, but from 8 to 14 December 2000 with the ranges for A (along shelf) -0.1 to 0.5 (blue to red) and B (across shelf) -0.1 to 0.2 ms^{-1} (blue to red) respectively. The Rottnest Island wind data had gaps on 10 and 14 December. Sea level was steady and was omitted from the Figure.

that in some cases drove the current in anticyclonic loops and they were separated by roughly 43 and 36 hours. The associated speeds reached 0.3 ms^{-1}.There was warming associated with each of the oscillations: for the first it was 1°C peak to trough; then 0.7°C for the second; and 0.3°C for the third.

Sea-land breeze effects

The daily oscillations in temperature in December 2000 noted earlier are seen in Figure 12 to be closely tied to northward wind stress and the along-shelf and cross-shelf current components. The current components show considerable complexity, with contrary flows at different depths being quite common. What are the links between the daily cycles of wind stress, currents and temperature at the instrument?

To address this we have selected a one-day interval and drawn PVDs for the currents and also a PVD for the Rottnest Island wind stress (Figure 13A), since that is likely to be the force driving the daily oscillations. The wind stress PVD "progressed" roughly northward, due to strong sea breeze forcing from about 1100 to 2300 local time, together with a weaker land breeze for the remainder of the time. Similar behavior was seen on other days. While there was strong positive along-shelf flow at all depths, the cross-shelf flows were noticeably oscillatory and apparently out of phase at different depths. The daily warm half cycle occurred during the sea breeze.

To examine the daily-varying currents we calculated the steady hourly flows from the daily progressions and subtracted these from the observed currents and prepared new PVDs (Figure 13B). These were closed loops around which the progressions were anticlockwise. The "hour hands" from the origins to midway around the perimeters show how the upper waters were out of phase with the lower waters: compare the top and bottom PVDs at 17 and 65 m. The phase difference would explain the contrary flows seen in the upper and lower waters in Figure 13A. There was also a phase difference between the wind stress and the current, with the stress leading the current at 17 m by about 4 hours. The temperature information on the deepest PVD – circles indicating the warm half cycle of the temperature fluctuation — suggests the possibility that warm water from the shelf moved offshore past the mooring for a half cycle and then cool water moved inshore past it for the other half cycle. For comparison, the same temperature information has been added to the PVD for 17 m depth.

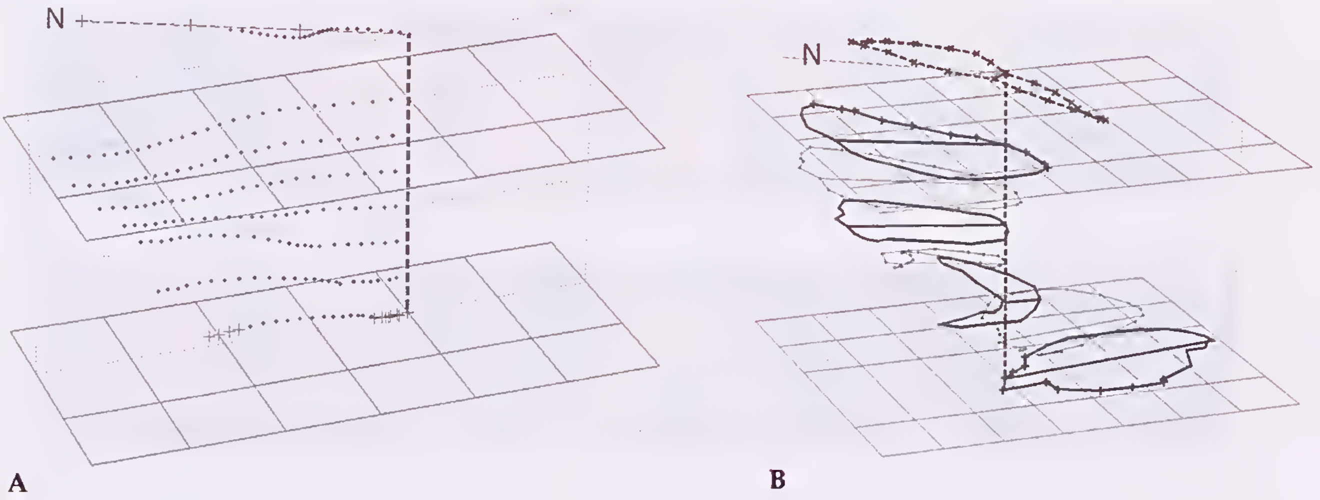

Figure 13A. As for Figure 6A, but for one day from 1000 UTC (1800 WAST) 11 December 2000 to 0900 UTC (1700 WAST) 12 December 2000 and with pluses on the lowest PVD (65 m depth) PVD indicating when the temperature exceeded 18.7°C.
Figure 13B. As for Figure 13A, except that the steady translations over the one day period have been removed and the mesh size is 1x1 km. The daily warm half cycle (T>18.7°C) is marked by the pluses on the PVDs for 17 and 65 m depth and the "hour hands" on each path go from the origin to the 12 hour point. The angled dashed line at the top indicates north.

Discussion

This is the first uninterrupted year-long record of currents on the continental shelf of temperate Western Australia. It covers 13 x 4 m depth intervals (3/4 of the water column at the 70 m isobath) and temperature was measured at the instrument. Prior to this the best record is that from mooring site D2 at the 108 m isobath off Dongara as part of the LC Interdisciplinary Experiment, LUCIE (The Lucie Group, 1988). That mooring had four current meters at different depths and with two deployments covered the period September 1986 to August 1987, albeit with a 2 ½ week gap. We will refer to the results in this discussion. The three moorings along the Two Rocks line in 2004/05 also yielded important information (Fandry et al., 2006).

As expected, the dominant seasonal features of the present ADCP record are the LC in winter and the CC in summer. These currents were at times highly variable due to wind and other forcing; they reached speeds of 0.9 ms^{-1} and 0.6 ms^{-1}, respectively. The wind-driven CC ceased at times of diminished northward wind forcing: if this forcing became smaller than ~0.06 Nm^{-2} then it seems as if the background north to south pressure gradient drove an unseasonal LC. On one occasion in winter the LC (at the mooring) ceased and there was a week-long northward flow that could not be related to wind forcing. It is possible that an anticyclonic eddy from the open ocean was having an effect on the shelf currents. Such interactions have been studied by Moore et al. (2007) with anticyclonic eddies being found to entrain shelf waters with relatively high concentrations of chlorophyll *a*.

The flow of the CC is known from satellite imagery (Pearce and Pattiaratchi, 1999) to be associated with the appearance of cool upwelled water on the continental shelf. Progressive vector diagrams, which tend to smooth over current variability, did show onshore flow and cool water at the ADCP in December 2000. However, there was no persistent onshore flow at 65 m nearest the bottom. It was only further up in the water column that steady onshore flow was experienced: it was strongest at the 49 m depth bin where the flow made an angle of 17° with the shelf edge. With decreasing depth the angle decreased, became zero at 33 m and 7° offshore at 17 m depth (the shallowest bin). The 1°C temperature oscillation experienced each day may have been due to forcing from the sea-land breeze cycle and the close proximity of a front between warm shelf and cold slope water. This will be discussed below.

The annual temperature range measured at the ADCP was 18–22°C, with brief excursion above and below. At the LUCIE D2 site, almost 40 m deeper and at the shelf edge, the range was 19–22°C. In both cases the presence of the tropical LC waters served to counteract seasonal cooling and held the water temperature at 22°C from March until July.

Monthly progressive vector diagrams showed, somewhat surprisingly, that the LC, from March, was strongest at depth where it was directed as much as 40° off the shelf. Since there was no compensating flow nearer the surface – unless it was in roughly the upper 15 m – there must have been on-shelf flow somewhere north of the site, perhaps even related to the geometry of the Abrolhos Islands. The LUCIE D2 measurements also showed increasing off-shelf flow with increasing depth, but the current speed decreased with depth.

The currents throughout the record changed continuously on time scales up to several days, as can be seen in the cross-shelf current plot in Figure 2. By restricting our time "window" to several days and selecting a number of examples we were able to observe effects due to changes in wind forcing, shear and rotation with changing depth, a type of oscillation with a time scale 15–45 hours that at times created anticyclonic loops as much as 10 km across, and shear due to the sea-land breeze cycle.

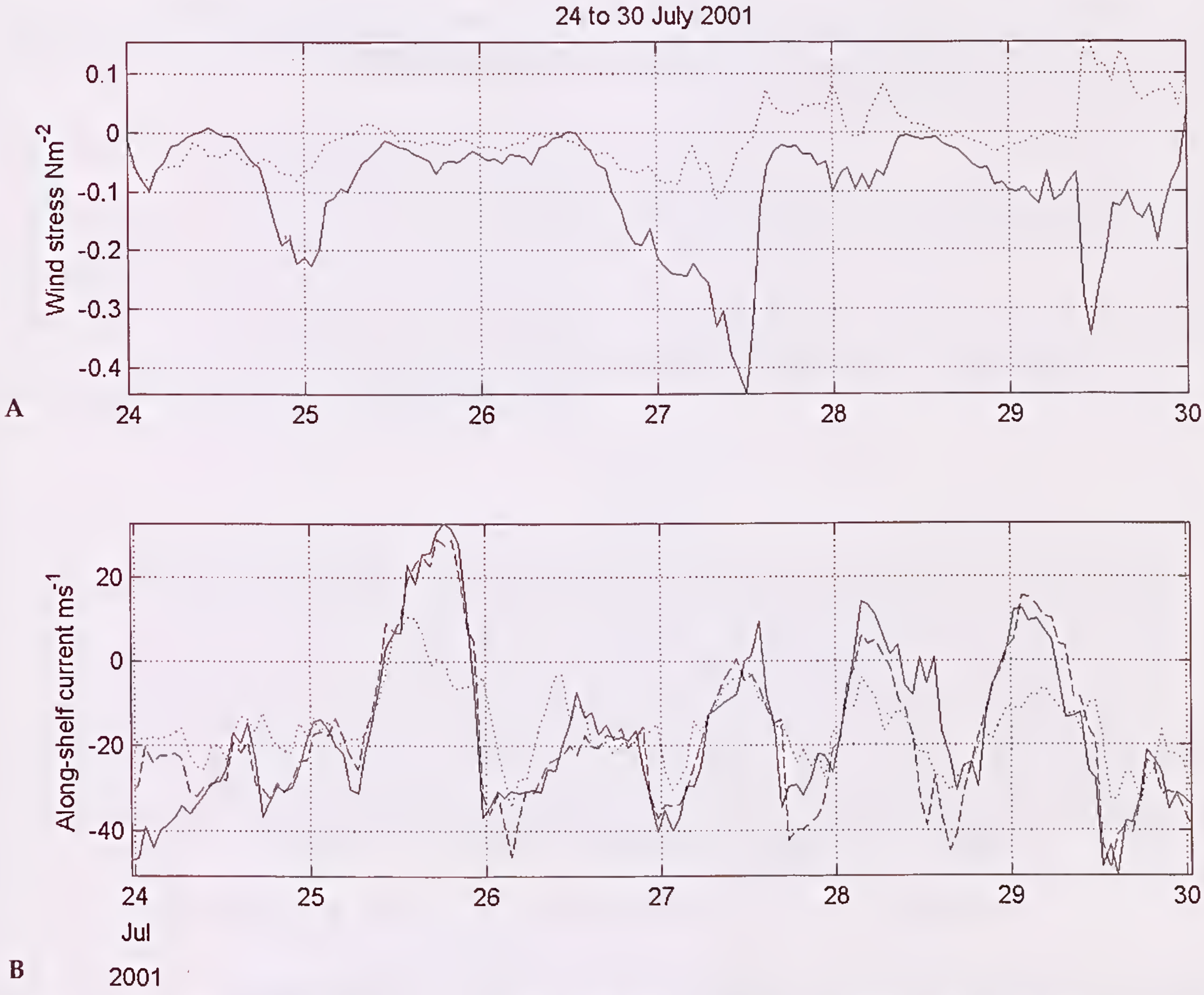

Figure 14. Time series of, A) wind stress showing north-south (full line) and east-west (dashed line) components and, B) along-shelf current at 17 m (full line), 41 m (dashed line), and 65 m (dotted line) depth.

The 1–2 day oscillations and loops are difficult to interpret with data from only a single point. Figure 14, the time series for 24–30 July 2001 to accompany Figures 11C and D, shows that the strong southward wind pulses that punctuated calm conditions bore little relationship with the current oscillations marked by the loops and cusps seen in the PVDs. The generation region and mechanism and the propagation direction and speed for these "waves" will have to await further observations from mooring arrays.

The sea-land breeze cycle generated anticlockwise motion through the water column – seen when the steady translation was removed from the motion – with the lower waters being out of phase with the upper ones. The loops that were generated were up to several kilometres across. It would seem that the 24-hour period wind forcing, which was also anticlockwise, served to drive baroclinic inertial waves, since at this latitude the inertial period is about 24 hours.

These inertial oscillations, the larger cross-shelf movements associated with the ~15–45 hour waves discussed earlier, and episodic cross-shelf motions will be important in the life cycles of marine creatures.

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Oceanic processes and the recruitment of tropical fish at Rottnest Island (Western Australia)

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Abstract

Transport processes relating to the observed annual "pulse" of tropical fish larvae arriving at Rottnest Island each autumn are examined using historical current measurements in the Leeuwin Current near the Abrolhos Islands and along the continental shelf just north of Perth. Observations of two common damselfish between 1977 and 2002 (with enhanced detail of fish size categories from 1994) show that the bulk of new recruits settle at Pocillopora Reef in March/April, a time when the Leeuwin Current is strengthening and the Capes Current is waning. Very large recruitment pulses in 1999 and 2000 were in *La Nina* years when the Leeuwin Current was very strong and water temperatures were at record high levels, but a third relatively strong pulse in 1995 was during an *El Nino* period with a weak Leeuwin Current (albeit with elevated ocean temperatures). Both advection and temperature therefore appear to play significant roles in recruitment at Rottnest Island, while biological factors such as food and predation during the pelagic stage must also be considered. The potential role of algal rafts in enhancing larval transport and survival may be important in the recruitment process and needs further research.

Keywords: Leeuwin Current, oceanic processes, larval transport, fish recruitment

Introduction

Many, if not most, marine fish species undergo a pelagic larval migration phase as part of their life cycle. This process serves to disperse the larvae away from the spawning area, leading to potential recruitment/ colonisation at distant locations (depending on the duration of the pelagic phase) where they settle and complete their life cycle.

Ocean currents accordingly play a major role in the dispersal process, and off Western Australia the Leeuwin Current is the dominant boundary current, flowing southward down the Western Australian coast and then eastwards along the south coast (Cresswell & Golding 1980).

The existence of a warm offshore current had been postulated as early as the 1890's by Saville-Kent (1897) to explain the presence of tropical species at the Abrolhos Islands. The progressive southwards shift from tropical to temperate fauna was identified by Michaelsen (1908), who surveyed the nearshore waters from Shark Bay to Albany in 1905, and he too felt that a warm southward current must be responsible for the presence of *Pocillopora* corals as far south as Rottnest Island. Hodgkin *et al.* (1959) recognised the distinction between the "Flindersian" (warm temperate) marine species along the mainland coast and on some sections of Rottnest Island against the more "Damperian" (tropical) species found dominantly on the western end of the Island. Likewise, the increased abundance of tropical molluscs on the western end of the Island compared with the eastern coast was attributed to the newly-discovered Leeuwin Current by Wells (1985).

Rottnest Island lies some 18 km west of Fremantle (Figure 1) near the edge of the continental shelf and is frequently bathed by Leeuwin Current waters either directly (when the Current is flowing along the outer shelf) or indirectly (by cross-shelf processes when tongues of warm Leeuwin Current water penetrate shorewards – Pearce *et al.* 2006a). Clearly, the Island is in an interesting overlap zone where both tropical and temperate marine species are encountered, partly as a result of the Leeuwin Current which acts both as a conduit for the southward transport of tropical fauna and also maintains relatively high temperatures around the Island.

Exploratory surveys of the reef fish distribution along the Western Australian coast (Hutchins 1977, 1994, 1997a) confirmed a progressive change from dominantly tropical species in the north to a largely warm-temperate component in the south. Tropical forms were found to make up 64% of the species at the Abrolhos Islands (29°S – Figure 1) while at Rottnest Island only 30% of the species were of tropical origin and 53% warm-temperate (Hutchins 1994), and there was also a marked reduction

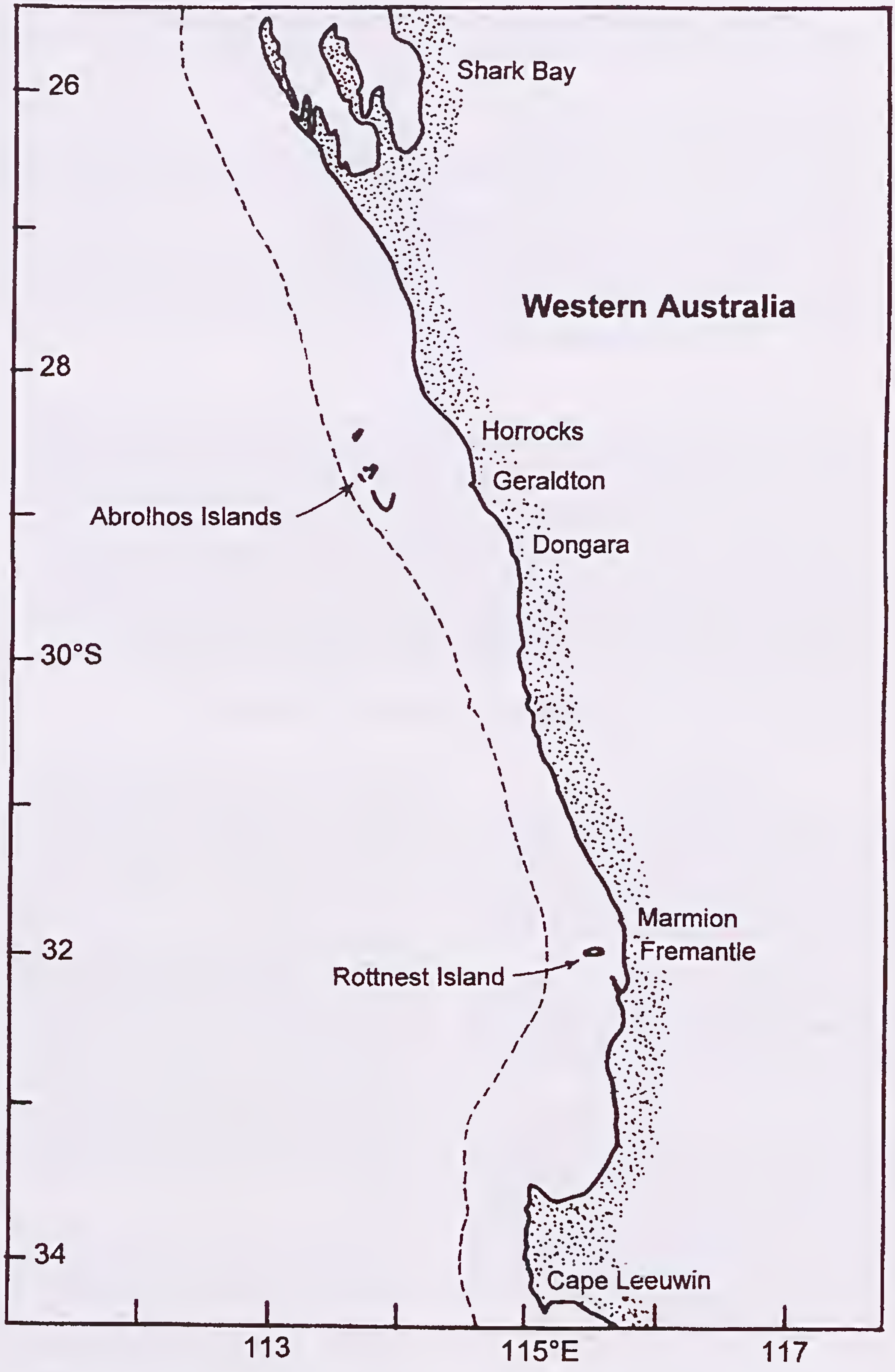

Figure 1. Location chart showing the main sites mentioned in the text. The dashed line marks the edge of the continental shelf.

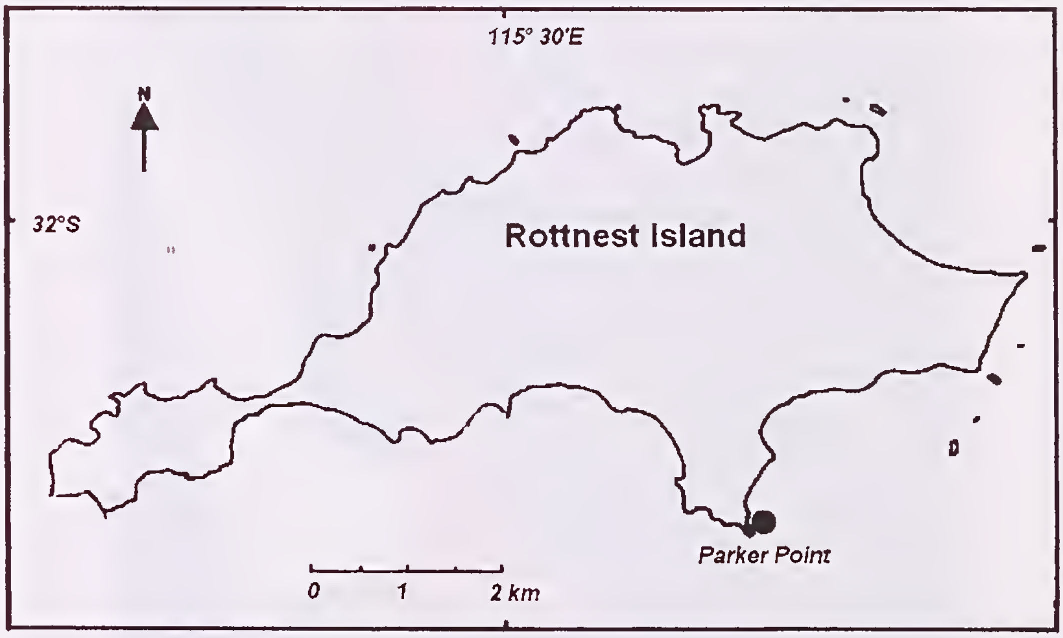

Figure 2. Location chart of Rottnest Island showing the observation site at Parker Point.

in tropical species between these offshore islands and the adjacent mainland coastal waters at the same latitude (Hutchins 1994). In a more recent study, Watson & Harvey (2009) found tropical species made up 66% of the fish fauna at the Abrolhos compared with only 2% at Rottnest Island.

Observations of tropical fish in the shallow bays around Rottnest Island over the past 25 years have revealed the annual arrival of larval recruits each autumn. Hutchins (1991) found that the tropical fish fauna tend to concentrate along the southern coasts of the Island, and in particular in the area near Pocillopora Reef off Parker Point (Figure 2). Here, there is a conspicuous reef of the coral species *Pocillopora damicornis* which attracts newly arrived recruits and also supports longer-term populations of tropical (and other) fish. An influx of very small juvenile fish commences in autumn and continues spasmodically until as late as November in some years (Hutchins 1991), but there are large inter-annual differences in settlement numbers.

Two common damselfish (*Abudefduf sexfasciatus* and *A. vaigiensis*) are among the most visible and abundant recruits at Parker Point. These 2 species have been found on reef systems from the Dampier Archipelago (21 °S – Hutchins 2003), at Ningaloo Reef (22 °S – Hutchins 1994), Shark Bay (25 °S), and offshore at the Houtman Abrolhos Islands (29 °S: Hutchins 1994; Hutchins 1997b). Rottnest Island appears to be their southernmost habitat along the Western Australian coast, based both on the published literature and by personal observation by Hutchins (hereafter denoted BH). While Hutchins (1997a, 1997b) has observed breeding behaviour at the Abrolhos Islands, no breeding activity has been observed at Rottnest Island (BH) and so there is presumably no local recruitment of these 2 species at the Island.

A survey of larval fish along a transect some 50 km north of Rottnest Island (Muhling & Beckley 2007; Muhling *et al.* 2008; Beckley *et al.* 2009) found that the temporal and spatial structure of larval fish assemblages was closely linked with the seasonally-varying current system and water mass structure across the shelf. During this study, three *Abudefduf* larvae (species not documented) between 2.6 and 3.3 mm in length were caught at mid-shelf in water depths of about 40 m in early April 2004 (Muhling 2006; pers.comm.), which coincides with the timing of new recruits at Rottnest Island.

This paper presents the observations of larvae and juveniles of the two *Abudefduf* species at Parker Point in relation to oceanographic processes off south-western Australia. Three stages of the life cycle (dispersal, alongshore transport, and settlement) are examined in some detail. In particular, mechanisms of larval transport are explored using existing knowledge of the Leeuwin Current and the flow on the continental shelf, and a simple web-accessed trajectory model (Aus-Connie: Condie *et al.* 2005) is used to assess connectivity between the Abrolhos Islands and Rottnest Island.

The current system along the Western Australian coast

Because of the importance of the alongshore and cross-shelf advection processes in the dispersal of marine larvae, we briefly review the seasonality and main characteristics of the current systems off Western Australia. Small-scale, more localised circulation patterns near the Abrolhos and Rottnest Islands are dealt with in the Discussion.

Sea-surface temperature images from the Advanced Very High Resolution Radiometer (AVHRR)) on the NOAA satellites show the Leeuwin Current flowing strongly southwards as a jet along the shelf break and outer shelf during the winter/spring months, often with mesoscale meanders/eddies sporadically carrying the

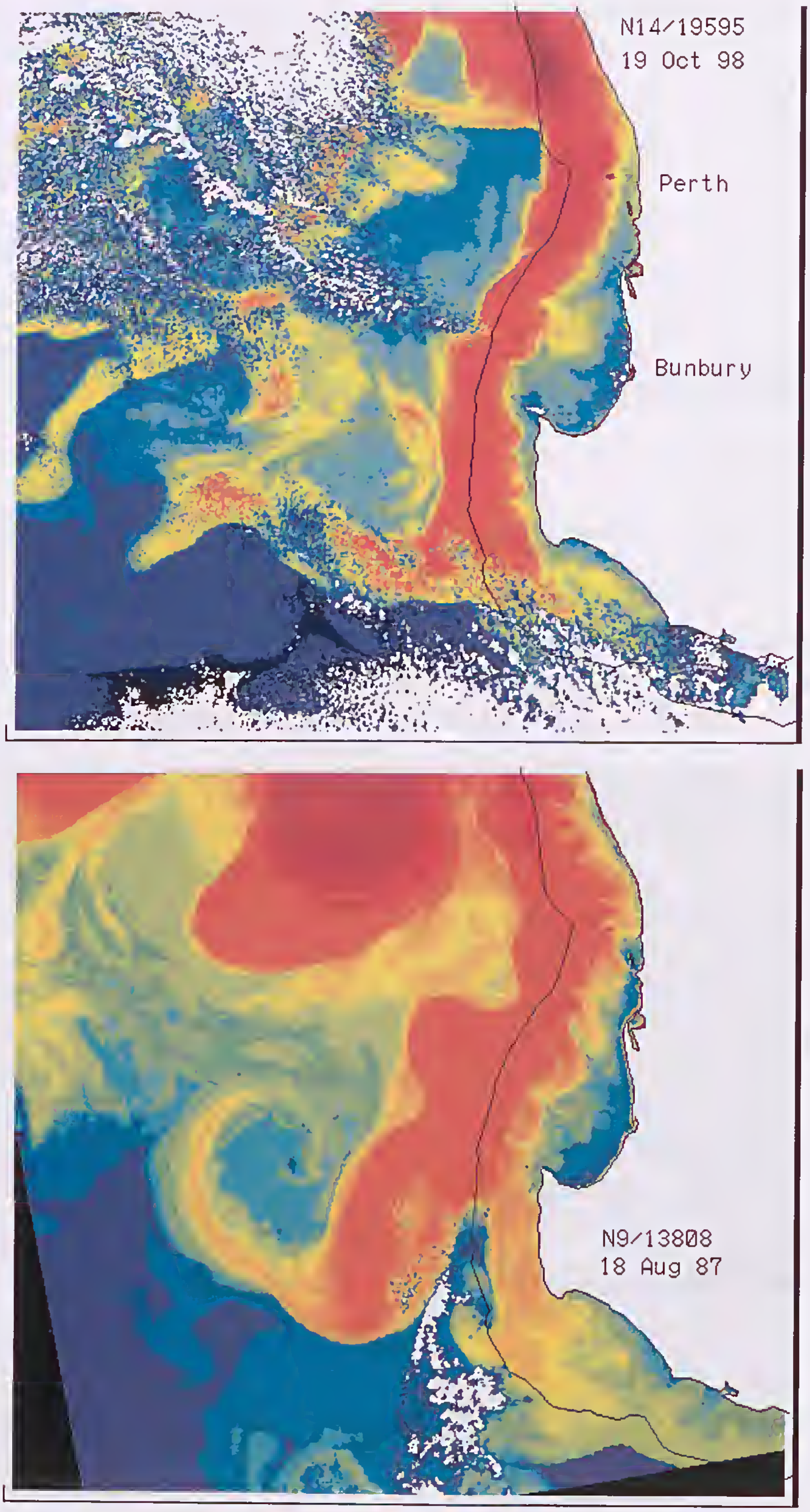

Figure 3a & b. Sea-surface temperature (SST) satellite images from the Advanced Very High Resolution Radiometer (AVHRR) on the NOAA series of satellites in (upper panel) October 1998 and (lower panel) August 1987. The brightness temperatures in AVHRR Band 4 are shown (not corrected for atmospheric effects). The temperature colours are different in each image because they have been enhanced to illustrate the desired features of the flow patterns; they vary from the warmest water (in red/orange) through yellow/green to the coolest water in blue. Images by courtesy of CSIRO Marine and Atmospheric Research and the Western Australian Satellite Technology and Applications Consortium (WASTAC).

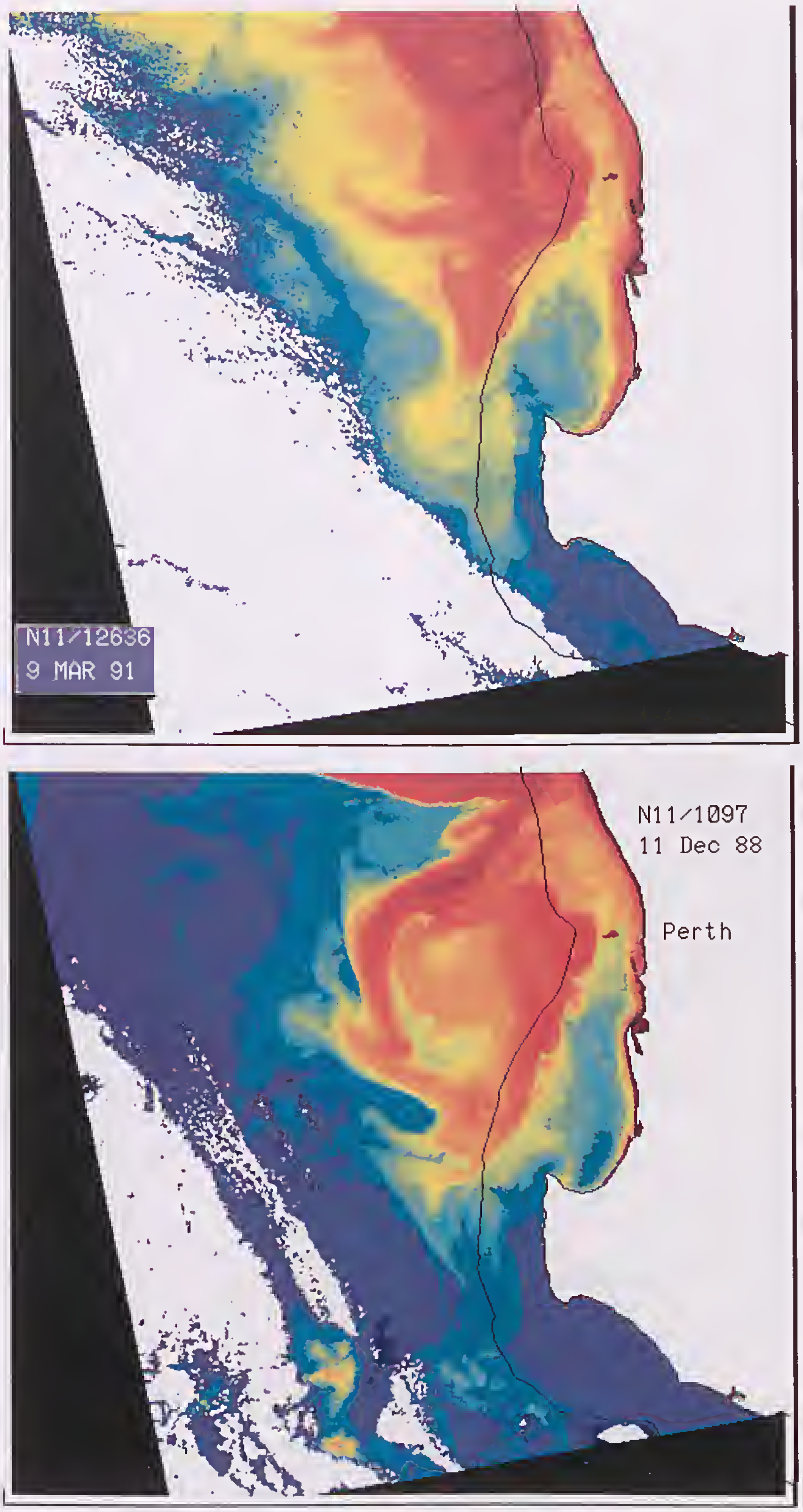

Figure 3c & d. As for Figure 3a & b, but for (upper panel) March 1991 and (lower panel) December 1988.

warm waters offshore in large (~ 200 km) loops (Figures 3a,b). In summer, the Leeuwin Current weakens in response to the strong southerly (northward) wind forcing and the coastal Capes Current can be seen pushing cooler water northward along the inner and mid-shelf (Pearce & Pattiaratchi 1999; Gersbach *et al.* 1999; Figure 3c). On occasion, the large eddies can temporarily distort the normal southwards flow of the Leeuwin Current – note the 150 km diameter anticlockwise eddy between Perth and Cape Naturaliste in Figure 3d, causing northward flow along the shelf-break past Rottnest Island.

On a more local scale, smaller (~ 10 to 20 km) tongues of Leeuwin Current water are evident penetrating shorewards across the continental shelf (*e.g.*, Figure 3b), indicating an active mechanism for the cross-shelf exchange of water and hence planktonic larvae. In addition, Figures 6 and 8 in Pearce *et al.* (2006a) show that bands of warm Leeuwin Current water can curl in towards Rottnest Island from the north and also wrap around the southern shore on occasion, thus providing a mechanism contributing directly to recruitment at the Island itself.

There have been few moored current measurements in the Leeuwin Current. During the 1986/87 Leeuwin Current Interdisciplinary Experiment (LUCIE: Smith *et al.* 1991; Church *et al.* 1989) current moorings off Dongara (Figure 1) showed the Leeuwin Current flowing persistently southward between February and June 1987, with near-surface speeds of 50 cm/s to 1 m/s (Boland *et al.* 1988). At other times, there were bursts of southward flow at similar speeds punctuated by brief and much weaker northward current reversals. Feng *et al.* (2003) have shown that the Leeuwin Current transport is greatest in winter but the mean surface current peaks in April.

Currents along the continental shelf exhibit a strong seasonal pattern which is largely driven by local wind forcing. During the summer months, the Capes Current (Pearce & Pattiaratchi 1999; Gersbach *et al.* 1989) flows northward at 5–15 cm/s (Steedman & Associates 1981; Cresswell *et al.* 1989; Pattiaratchi *et al.* 1995; Pearce *et al.* 2006a) although speeds of 30 cm/s can be experienced under strong southerly wind conditions. In winter, on the other hand, the currents are largely southwards with speeds of between 5 and 20 cm/s (Steedman & Associates 1981; Cresswell *et al.* 1989; Pattiaratchi *et al.* 1995; Pearce *et al.* 2006a). In all seasons, current reversals and shorter-term pulses of current of up to 50 cm/s (1 knot) can occur.

Data sources and processing

Oceanography/meteorology

Because of the established link between the Leeuwin Current and El Nino/Southern Oscillation (ENSO) events (Pearce & Phillips 1988), monthly values of the Southern Oscillation Index (SOI – an indicator of the intensity and duration of ENSO phenomena, based on the difference in atmospheric pressure between Tahiti and Darwin) were obtained from the website http://www.bom.gov.au/climate/current/soihtm1.shtml (verified August 2007).

Coastal sea level can be used as an index of the "strength" of the Leeuwin Current (Pearce & Phillips 1988; Feng *et al.* 2003), so monthly sea level data for Fremantle were acquired from the National Tidal Centre in Adelaide. Monthly anomalies were derived by subtracting the overall mean seasonal cycle from the individual monthly sea levels, and 3-month moving averages were taken to smooth smaller-scale variability and emphasise the dominant ENSO-related fluctuations.

Monthly sea surface temperatures (SST) were obtained on a 1-degree latitude/longitude grid (approximately 100 km) from the Reynolds global dataset (Reynolds & Smith 1994). The selected grid was for the area 31° to 32°S, 115°E to the coast, generally reflecting open-ocean conditions immediately northwest of the island and hence including the Leeuwin Current. Monthly anomalies were derived and smoothed as for sea levels. Local water temperatures at Parker Point were taken from satellite-derived measurements between 1995 and 2001 by Pearce *et al.* (2006b), while the nearshore temperature cycle at the adjacent mainland coast was derived from temperature loggers off Marmion between 1990 and 1994 (Figure 1; Pearce *et al.* 1999).

Fish surveys

Visual surveys of the fish fauna in the nearshore waters of Rottnest Island were undertaken between 1977 and 2002. While observations were made in a number of bays along the southern and western coasts of the Island (Hutchins & Pearce 1994), it was found that the bulk of the recruitment occurred off Parker Point (Figure 2) and so most of the effort from 1994 focussed on Pocillopora Reef in Parker Point Marine Reserve. The water depth over the reef was 1 to 2 m, with some areas being exposed at low spring tides.

During each survey, a diver (BH) swam a grid pattern lasting about an hour along a transect which followed the extensive system of *Pocillopera* colonies and ended in the rocky shallows near the Parker Point headland. The survey route was always the same, giving a good coverage of the reefs in the study area, and was planned so that the chances of counting a fish twice was unlikely. 20 fish species were identified and counted (Hutchins & Pearce 1994), but in our analysis here only the damselfishes *Abudefduf sexfasciatus* (Scissortail Sergeant) and *A. vaigiensis* (Indo-Pacific Sergeant) were used as they were readily identifiable and they also remained in the open after settling (unlike those fish that tended to hide after settlement – Hutchins 1991; Hutchins & Pearce 1994). These tropical reef-dwelling fish are not endemic to Western Australia (Hutchins 1994) but are widely distributed in the Indo-Pacific region. Choat (1991) has classed them as omnivores, feeding largely on zooplankton and benthic algae. They have been recorded as both juveniles and adults at Rottnest Island but not at the adjacent mainland coast (Hutchins 1991). The Scissortail Sergeant can grow to a length of some 16 to 22 cm (Allen & Swainston 1988; www.fishbase.org; www.amonline.net.au/FISHES/fishfacts/fish/asexfasc.htm), while the Indo-Pacific Sergeant reaches a maximum length of 20 to 22 cm (Allen & Swainston 1988; www.fishbase.org; www.amonline.net.au/FISHES/fishfacts/fish/avaigiensis.htm).

In the earlier years from 1977, visual counts were made of the total numbers of selected species observed and the first observation of new recruits noted, but since 1994 the various stages of growth were visually classified into 6 categories, ranging from just after arrival (when they still retained their planktonic morphology) up to the sub-adult stage, are shown below:

Class/description	Standard Length SL mm	Total Length TL mm
a = minute juvenile with pelagic colouration/features	11–17	15–23
b = very small juvenile	19–26	25–36
c = small juvenile	30–40	40–55
d = juvenile	45–57	65–77
e = large juvenile	60–72	80–100
f = sub-adult (i.e., about to mature)	75 +	110 +

The change from one category to the next was somewhat subjective. The estimates for the Standard Length (SL, which does not include the tail) and the Total Length TL (including the tail) were based on measurements of a selection of the sampled fish. As *Abudefduf sexfasciatus* and *A. vaigiensis* have similar maximum lengths and there do not seem to be any obvious size differences in the early growth stages, we believe these categories are adequate for both species. Category "a" is the pelagic larval phase of the life cycle and "b" represents the first post-settlement juvenile stage, these 2 phases being the main focus of this paper. The smallest and largest individuals in the pelagic category "a" observed at Rottnest Island were about 17 mm and 23 mm TL respectively; the 15 mm TL fish (estimated age of about two weeks) was collected from floating *Sargassum* to the north of Rottnest. Most new recruits of the two *Abudefduf* species arriving at Rottnest had a transparent silvery colour, but they quickly developed dark bars on the body after settling. However, those that had spent some time under rafts of floating *Sargassum* could arrive at the island with the full juvenile colouration. Larvae that survived from the commencement of settlement in March or April usually reached the sub-adult stage by the end of the year. As no breeding activity was ever observed during any of the surveys at Rottnest Island (BH), we believe there was no recruitment from local populations and all new recruits must therefore have arrived from a northern source.

It was found that *Abudefduf* recruitment always occurred in the same locations (shallow areas with good protection from wave action) and the larvae preferred to settle in reef areas just below the water's surface: small juveniles were rarely found on reefs with depths of more than 1 m (at high water). The first recruits always arrived in the shallow protected reefs behind Parker Point headland and in many years that was the only location where recruits were found. The more exposed reefs in the study area only received recruits during periods of heavy settlement (such as 1995, 1999 and 2000 – see Results below), suggesting that the more favourable areas had become overcrowded. It appears therefore that the more exposed areas were less favourable to recruitment as in low settlement years new recruits were rarely found there, and certainly these areas had the greatest mortality during winter storms. The larger juveniles tended to move from their initial settlement sites in the reefs behind the headland to more exposed areas closer to the edge of the lagoon to feed as the flow of water (and presumably plankton) into the lagoon was greater there.

The number of sampling days at Parker Point was somewhat sporadic (Table 1), especially the period 1986

Table 1

Number of fish surveys per month at Parker Point Marine Reserve. Bolded-underlined entries are the months when new recruits were first sighted.

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1977			2						1			1
1978				**1**		1	1	1	1	2		1
1979	1		1		**2**		1	1				1
1980			**2**	1	1	1		1		1		
1981								1				1
1982				**2**		1	1			1		
1983	2	1	1	**1**	1	1	1		1	1	2	1
1984	1		2	**1**	1	2	1	1	1	1	1	2
1985	1	1	**2**		2	1	1		1	1		1
1986												
1987												
1988									1			
1989			1								1	
1990				1								2
1991			1	**3**	1			1			1	
1992	1	1	1	**2**	1	1	1	1		1	1	
1993	1			1	**1**		1	1		1	1	
1994			1	**4**	2	3		1	1	1	1	1
1995	2	1	**2**	1	1	2	1	1	1	2	1	1
1996	1	**1**	1	1	1	1		1		1	1	1
1997	1	1	**1**	1	2	2	1	1	1		1	
1998	1	1	1	**1**	2	1	2	1	1	1	1	1
1999	1	1	**4**	2	2	1	3	1	1	1	2	1
2000	**1**	2	1	2	1	2		1	1	1	2	1
2001	1	1	**2**	4	1	2	1	2		2	2	
2002	1	1	**2**		2				1		2	
2003				1								
Totals	16	12	28	30	24	22	16	17	13	18	20	16

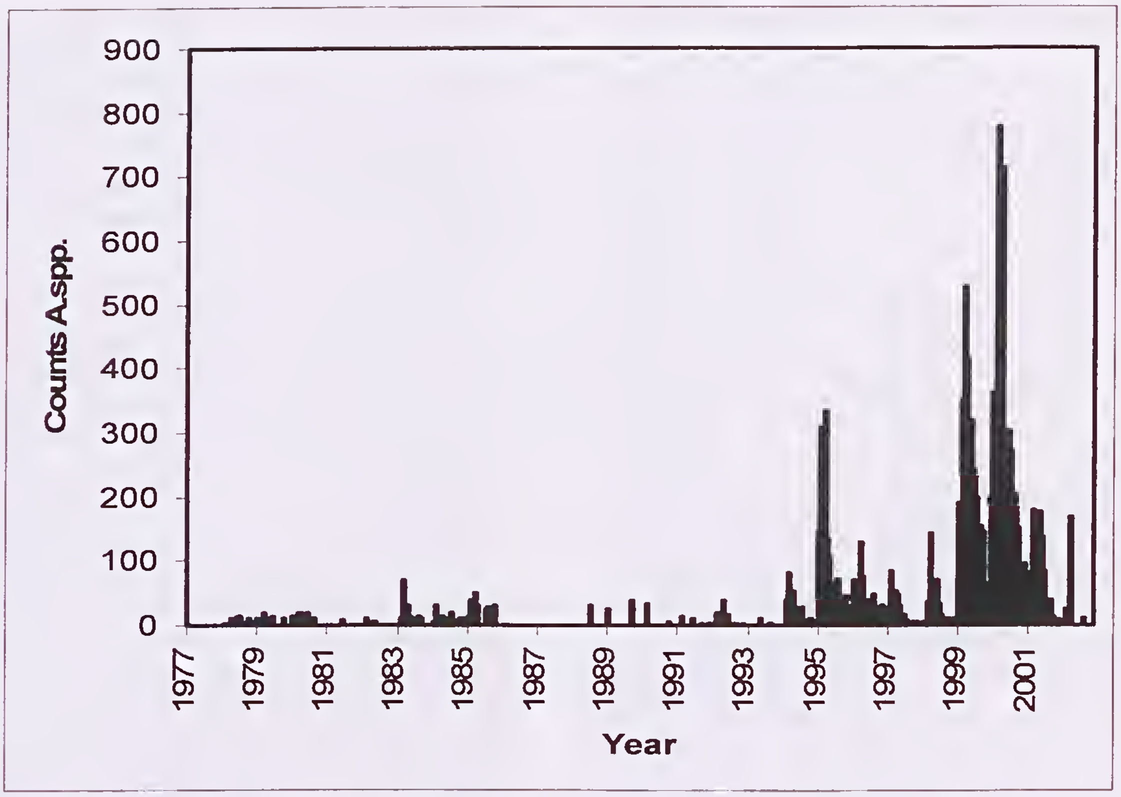

Figure 4. Numbers of all size classes of the two *Abudefduf* species (combined) at Parker Point from 1977 to 2002.

to 1990, due to diver availability, weather conditions, *etc.*, a total of 232 days of observations were undertaken.

Because of the irregular nature of the sampling, short-term (*e.g.*, daily) variability in larval abundance is not known but we believe that the observed larval and juvenile counts realistically reflect the general monthly abundance of the fish – this is borne out by the extended period (weeks to months) of the larval peaks shown below in Figure 5. These peaks in recruitment of the two *Abudefduf* species at Parker Point were matched by the arrival of large numbers of other tropical fish larvae both at that site and many other sites around the Island (BH personal observations); *Abudefdufs* were nearly always the first arrivals at any site. The most noticeable short-

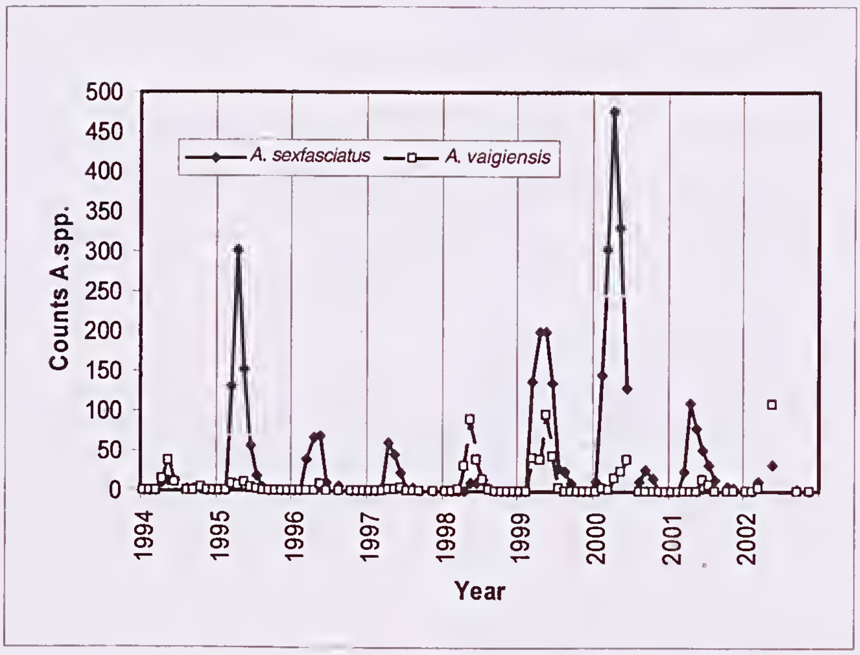

Figure 5. Numbers of category "a" and "b" larvae of the two *Abudefduf* species for the enhanced observational period 1994 to 2002, signifying the arrival of new recruits. Note that many of the monthly counts were very low (often <10 – see Figure 6) and are therefore indistinguishable from zero on this scale. Missing observations have been left blank.

term changes occurred after winter storms when numbers were always considerably reduced.

A consistent monthly time-series was derived by taking the maximum number of category "a" and "b" fish observed during all surveys in each month to facilitate further analysis against the monthly environmental data.

Results

Larval fish abundance at Parker Point

Abudefduf numbers at Parker Point were highly variable since the observations commenced in 1977. The fish were found there throughout the year (Figure 4), but two features dominated: a dramatic rise in numbers from 1995 onwards, and three major peaks of progressively increasing abundance in 1995, 1999 and 2000. Although the surveys effectively ended in 2002, anecdotal information from other observers indicated that these high recruitment levels have not been repeated since 2000. It is planned that regular observations will recommence during 2009 (BH).

The enhanced observations after 1994, which distinguished between the two *Abudefduf* species and also separated out the various size classes, showed that juveniles of *A. sexfasciatus* generally outnumbered *A. vaigiensis* and were by far the main contributors to the recruitment peaks (Figure 5). *A. vaigiensis* really only contributed materially to the 1999 peak, and small pulses of *vaigiensis* in 1994 and 1998 were not matched by *sexfasciatus*. The largest classes were assumed to be survivors from the previous year's recruitment based on their growth over the intervening year. These sub-adults and adults were observed to be very mobile, moving from reef to reef, and so could be difficult to locate from one survey to the next; as a result, the abundance of the later stages could vary tremendously between surveys and may have had little to do with survivorship.

Recruitment of category "a" and "b" juveniles clearly peaked between March and June, tailing off through winter and into spring (Figure 6). The monthly mean abundance (Figure 7c) shows that *A. sexfasciatus* tended to reach peak abundance earlier (March/April) than *A. vaigiensis* (May), although in 1998 the first *sexfasciatus* recruits were not spotted until July. Dramatic losses of fish could occur during the winter and spring months, such as between late June and mid-August 2000 when over 400 individuals disappeared in the northern reefs, probably as a result of storms.

The months when the first category "a" larvae of *A. sexfasciatus* and *A. vaigiensis* were observed in each year (when there were sufficient autumn observations) were:

Month	Year
January	2000
February	1996
March	1980, 1985, 1995, 1997, 1999, 2001, 2002
April	1978, 1982, 1983, 1984, 1991, 1992, 1994, 1998
May	1979, 1993

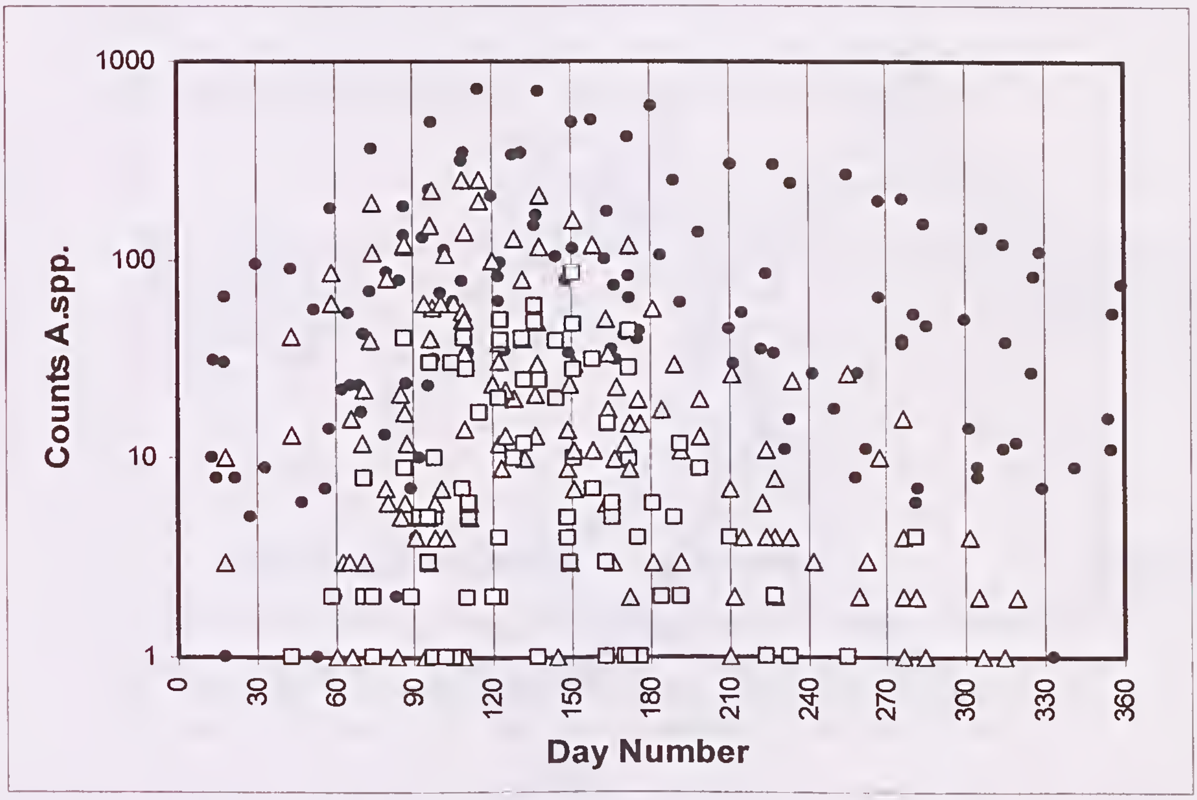

Figure 6. Numbers of the two *Abudefduf* species at Parker Point for the period 1994 to 2002 collapsed into a single calendar year (for plotting convenience divided into 30-day months). Small dots are the total counts (all size classes), while the larger open symbols are for category "a" and "b" larvae only: *A.sexfasciatus* triangles, *A.vaigiensis* squares. Note the log scale.

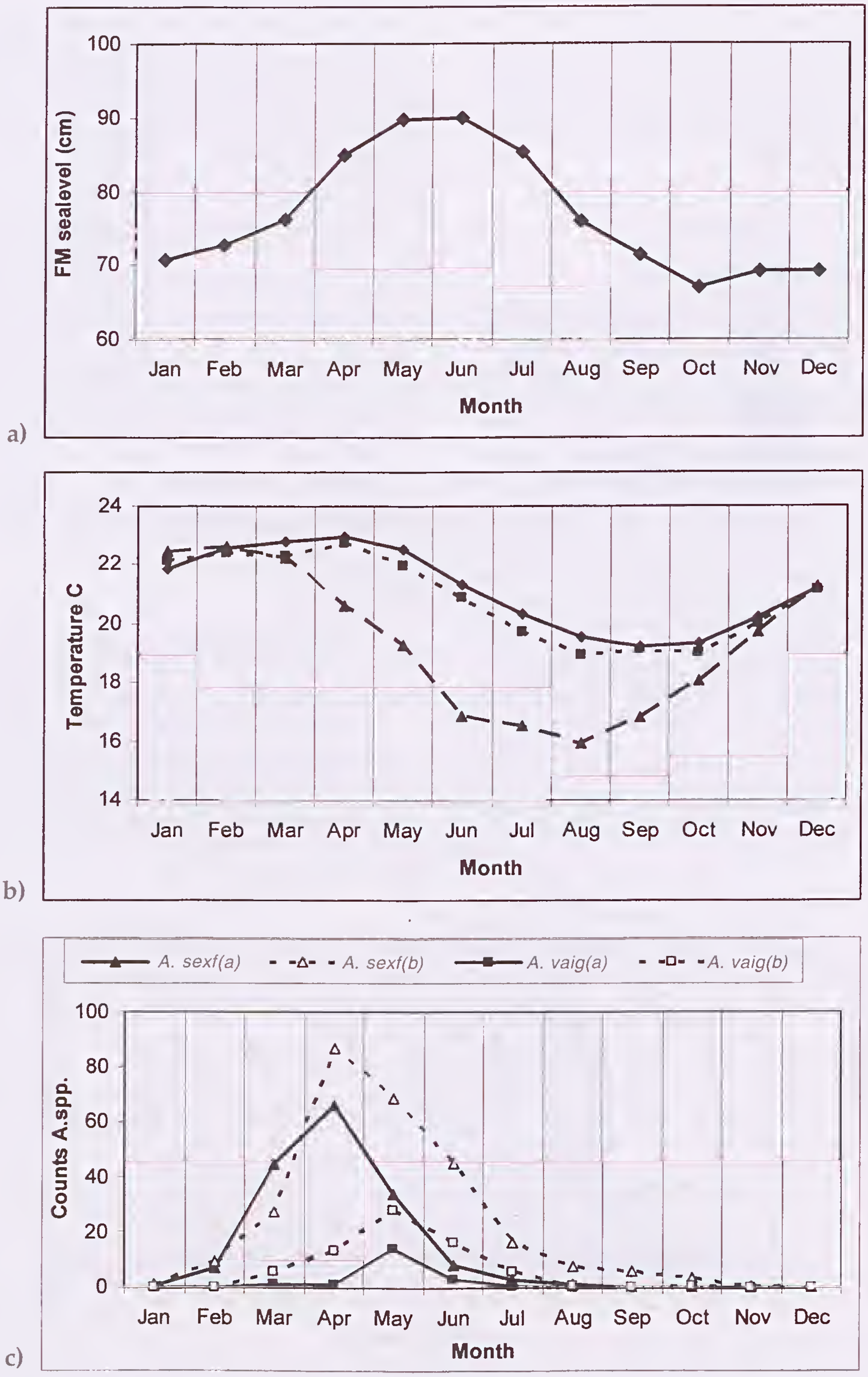

Figure 7. Annual cycles of (a) Fremantle sea level (representing the strength of the Leeuwin Current); (b) water temperature in the 1-degree square north of Rottnest Island (diamonds), at Parker Point (squares) and at Marmion (triangles); and (c) the abundance of categories "a" and "b" of *Abudefduf sexfasciatus* and *A.vaigiensis*.

Oceanography

Monthly mean values of Fremantle sea level (an index of the strength of the Leeuwin Current – Pearce & Phillips 1988) and water temperatures along the south-western Australian coast reflect both the influence of the Leeuwin Current offshore and the annual heat flux cycle in nearshore waters – Pearce *et al.* (2006a). The arrival of new tropical fish recruits at Rottnest Island (Figure 7c) coincided with the seasonal strengthening of the Leeuwin Current in March/April/May (Figure 7a) maintaining relatively high monthly-averaged temperatures of about 23 °C along the outer shelf, including Rottnest Island, well into May (Figure 7b). On average, the temperature dropped to 19 °C in September – an annual range of only 3 °C. By contrast, the nearshore water temperature peaks at 22.5 °C in February and then cools as a result of heat loss to the atmosphere, so by August the monthly average temperatures are down to about 16 °C (Pearce *et al.* 1999), representing a mean annual range of 6.5 °C. Individual temperatures can be as low as 13 °C during the winter months (ibid.), almost certainly too low for survival of tropical fish (BH).

At inter-annual scales, previous studies (*e.g.*, Pearce & Phillips 1988) have demonstrated that there is a generally close relationship between the monthly Southern Oscillation Index (SOI), Fremantle sea level (FMSL) and sea surface temperature (SST). Over the 26-year period 1977 to 2002, the correlation between the SOI and FMSL anomaly was 0.719 (312 observations), while that between the FMSL and SST anomalies (252 months from 1982 to 2002) was also 0.719 – these are both highly significant at the 99% level (Snedecor & Cochran 1980). During ENSO periods with a low SOI, sea levels were low (implying a weak Leeuwin Current – Feng *et al.* 2003) and the sea surface temperatures were correspondingly lower than average, while *La Ninas* were associated with high sea levels (stronger Leeuwin Current) and warmer water.

As seen in Figure 8, the period of enhanced fish observations from 1994 was preceded by an extended ENSO event (or series of events), and there was also an intense episode in 1997/1998 and a weaker one in 2002/2003. 1996 and 1999/2000 were both very strong *La Nina* periods with high sea levels and record high temperatures. There was an anomalous period in 1994/early 1995 when sea level and SST were opposed: the water was comparatively warm even though the Leeuwin Current was weak (low sea level), and there was also a similar but less pronounced event in late 1997.

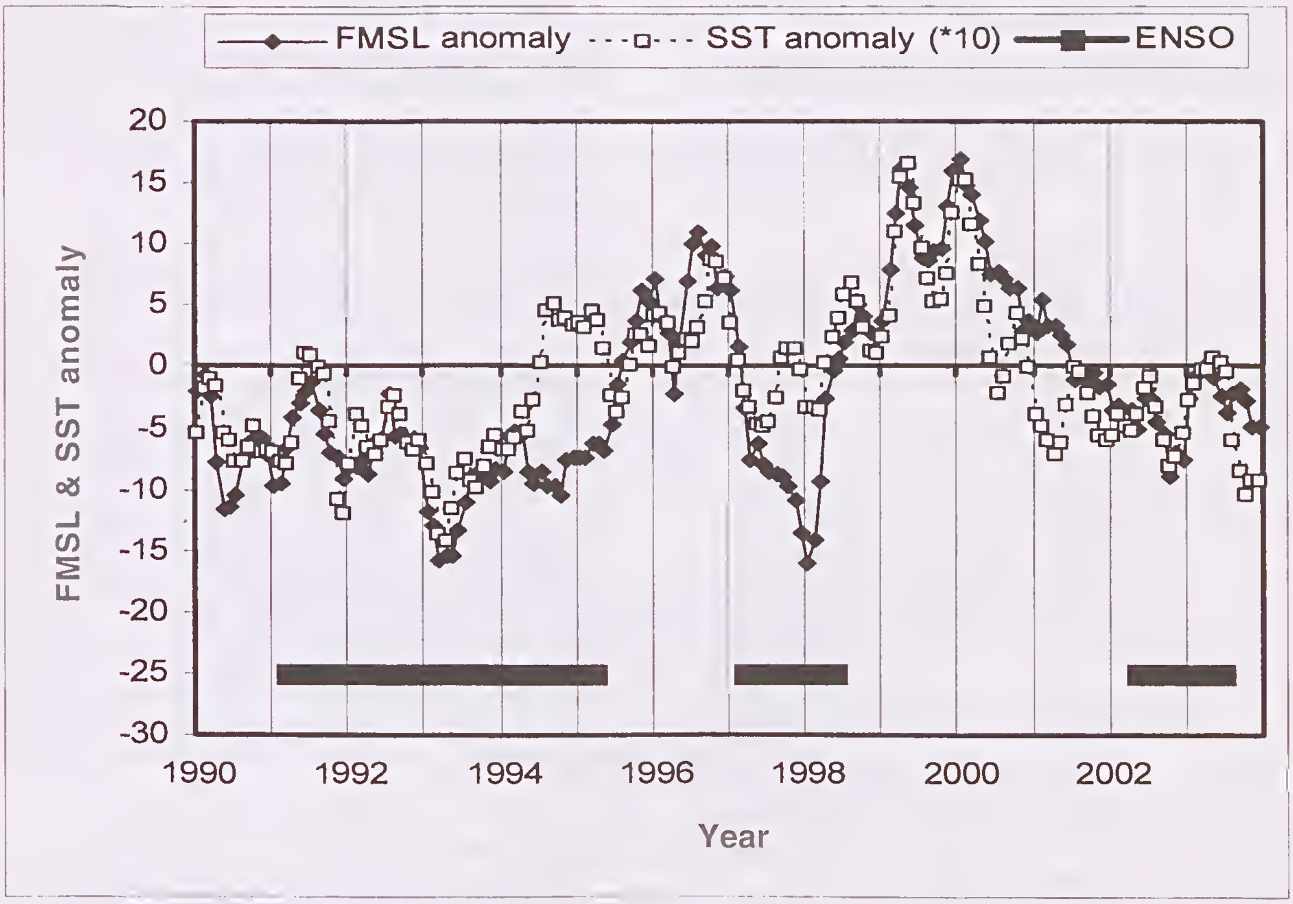

Figure 8. Monthly values of Fremantle sea level anomaly FMSL (see text) and the Reynolds sea-surface temperature anomaly SST (scaled by a factor of 10) from 1990 to 2003. A 3-month moving average filter has been applied to reduce small-scale variability. The solid bars represent ENSO periods.

Discussion

The duration of the pelagic phase is obviously crucial to the distance the larvae can travel before settling. Wellington & Victor (1989) used otolith daily growth increments to estimate the pelagic larval duration of *A. sexfasciatus* as 17.3 days (range 16 to 18 days) and 18.3 days (17 to 20) for *A. vaigiensis*. These are slightly shorter than Thresher *et al.'s* (1989) estimates of 19 to 27 days for *vaigiensis*, but a number of environmental factors can alter the larval growth and duration (Bergenius *et al.* 2005) so we will use 20 days in this paper.

Although many biological and oceanographic processes will play a role in successful recruitment of larval fish, we here focus on the role of the current system on the transport of *Abudefduf* larvae to Rottnest Island. To this end, three distinct stages of the life cycle are examined:

a) hatching and dispersal from the Abrolhos Islands;

b) southward transport in the Leeuwin Current and/or continental shelf currents;

c) settlement and recruitment at Rottnest Island.

The historical current measurements presented earlier are used to quantify the alongshore advective phase (b); while they were not co-incident with the significant larval settlement events found at Rottnest, they are used to provide an estimate of the likely transport rates of the larvae. In applying these results, we will use the convenient "rule-of-thumb" that 1 cm/s ~ 1 km/day – this is accurate to about 15%.

There is little information on the specific life histories of *Abudefduf sexfasciatus* and *A. vaigiensis* in the literature, so we have made use of whatever published information is available on damselfishes generally together with BH's local observations.

a) Dispersal from the Abrolhos Islands

Hutchins (1997a) defined a breeding population as one with a reasonable number of individuals representing most size classes. He found breeding populations of the two *Abudefduf* species at Shark Bay during a survey in May 1995 and at the Abrolhos Islands in February and May 1994, but no evidence of breeding at Rottnest Island. Nest-guarding behaviour was very evident at the Abrolhos Islands during the February survey (BH) and probably contributed to some local recruitment. Nevertheless, Hutchins (1997a) has suggested that the Abrolhos populations may also be maintained by transport via the Leeuwin Current from source regions further north such as Shark Bay (25°S) and perhaps even Ningaloo (22°S).

Hutchins' (1994) surveys at the Abrolhos Islands were centred on the Wallabi and Easter groups; *Abudefduf sexfasciatus* is listed as one of the 10 most abundant species there. The most diverse fish faunas were found on relatively sheltered reefs bordering the passages between the island groups and hence subject to the currents flowing between the islands.

As early stage *Abudefduf* larvae can be found off Rottnest Island for much of the year (Figure 6), spawning at the Abrolhos must also be spread over the seasons. However, the major pulse of new recruits arriving at Rottnest in March/April of most years suggests that a major spawning event may occur at the Abrolhos in February/March and that both environmental factors and food/predation must be particularly favourable for survival at this time of year.

The eggs are laid in patches on reef substrate and embryonic development occurs over 3 to 6 days (Wellington & Victor 1989). The eggs are buoyant and when they break free from the reef they rise into the water column; after a few days the larvae hatch and undergo the pelagic migration phase (see (b) below). These early larvae have limited swimming ability and are therefore largely planktonic, being at the mercy of ocean currents for dispersal away from the Islands.

Cross-shelf currents of 5 to 10 cm/s (Cresswell *et al.* 1989; Pearce & Phillips 1994) could move the larvae either offshore into the Leeuwin Current or shorewards into the seasonally-reversing current system on the continental shelf. Because, however, the summer wind regime at the Abrolhos Islands is strongly from the south (with a diurnally-varying sea breeze component – Pearce 1997; Gaughan & Mitchell 2000) resulting in a net offshore Ekman drift of the near-surface waters, it is in fact most likely that the larvae are carried offshore into the Leeuwin Current regime.

Larvae have been observed using floating objects and *Sargassum* rafts (Dempster & Kingsford 2004) both as a shelter and a source of food. Both larval and juvenile *Abudefduf saxatilis*, for example, have been observed under Sargassum weed in the North Atlantic Ocean (South Atlantic Fishery Management Council 2002). Hutchins (1994) reported that large areas around the Abrolhos Islands are covered with macroalgae, so any detached floating algal masses would also follow the wind-driven transport, possibly "collecting" larvae *en route* and hence assisting the dispersal process.

Water temperature can play an important role in all phases of the life cycle of fish, including their development, growth, swimming ability, reproductive performance and behaviour, and it is the early larval stages that are most sensitive to temperature changes (Munday *et al.* 2007). Warmer waters result in shorter incubation periods, increased growth rates, shorter planktonic durations and higher swimming abilities (*ibid.*). The annual mean temperature cycle at Rat Island in the Houtman Abrolhos group ranges from a summer peak of 23.7 °C in March down to 20 °C in August/September (Pearce 1997), so the presumed *Abudefduf* breeding and dispersal period is effectively at the time of peak temperature. It is worth noting that nearshore temperatures at Dongara on the adjacent mainland coast (Figure 1) peak at 24 °C in January/February and drop to 17.5 °C in July/August (Pearce *et al.* 1999), substantially cooler than those at the offshore islands during the winter months (as originally observed by Saville-Kent 1897).

b) Alongshore transport by the current system

The alongshore transport of fish larvae must be accomplished by the Leeuwin Current and/or the seasonally-reversing current system on the continental shelf. Although the mid- to later-stage larvae have a strong swimming ability, we will view them as passive drifters until they are within striking range of Rottnest Island when their swimming ability becomes important (section (c) below).

As shown earlier, the Leeuwin Current transports tropical waters southwards along the outer continental shelf and upper slope, most strongly during late autumn to early spring. Historical current measurements, however, indicate that the currents can be highly variable between months and years and do not always follow the traditional seasonal pattern. Southward current speeds in the Leeuwin Current itself can average between 40 and 60 cm/s over a month during the period of highest flow rate, with peak short-term speeds of double that. Any larvae which become entrained into the offshore eddy field (*e.g.*, Figure 3) are unlikely to return to the coast within the 3 week larval period and will probably perish, although under favourable circumstances those that are ejected near the shelf-break may survive to cross the shelf and settle at the Island (Holliday pers.comm.).

Mean current speeds on the continental shelf are more like 5 to 20 cm/s with a pronounced seasonal change between southwards flow in winter and a fairly consistent northward tendency (the Capes Current) in summer, with high levels of variability in both speed and direction in all seasons. Larvae originating at the Abrolhos Islands in February/March would probably encounter the Capes Current and so be carried northwards; later in the year the flow would more likely be southward and so aid migration towards Rottnest Island.

The speed/time relationship in Figure 9 shows the time required to reach Rottnest Island from the Abrolhos Islands, Shark Bay and Ningaloo Reef at different mean current speeds. Using the typical current speeds summarised above and assuming direct southward transport, the larvae would probably travel at speeds of 5 to 15 cm/s (*i.e.*, < 15 km/day) and they would not reach Rottnest Island within the pelagic larval duration of about 3 weeks. In the Leeuwin Current, however, where mean southward speeds are likely to be at least 20 to 30 cm/s, Abrolhos-derived larvae could easily reach Rottnest, while at net speeds of 50 cm/s Shark Bay and perhaps even Ningaloo emerge as possible larval sources. Clearly, the observed variability in alongshore current speeds can greatly affect the likelihood of larval migration from the three possible sources up the west coast and hence the recruitment at Rottnest.

A more quantitative indication of the probability of passive larvae spawned at the Abrolhos Islands reaching the vicinity of Rottnest Island has been assessed using the web-based larval transport model Aus-Connie (Australian Connectivity Interface; Condie *et al.* 2005 – http://www.per.marine.csiro.au/aus-connie, verified February 2008). The model simulates larval trajectories from a specific source region using satellite-derived sea level data (and derived near-surface currents) with modelled wind fields over the period 1995 to 1999 to examine the connectivity between the source and sink regions. The output is the probability distribution of planktonic larvae in 0.5 degree latitude/longitude squares over an assumed larval lifetime (in our case, the 30-day option in the model is the most appropriate for *Abudefduf* larvae of those available).

Defining the source region as the 1-degree block 28.5° to 29°S, 113.5° to 114.5°E centred on the Abrolhos Islands, we summed the probabilities of all squares south of 31.5°S and within about 1 degree of Rottnest Island on the (perhaps naive) assumption that this would encompass all the larvae that have reached or passed within 100 km of the Island within the larval lifetime. We

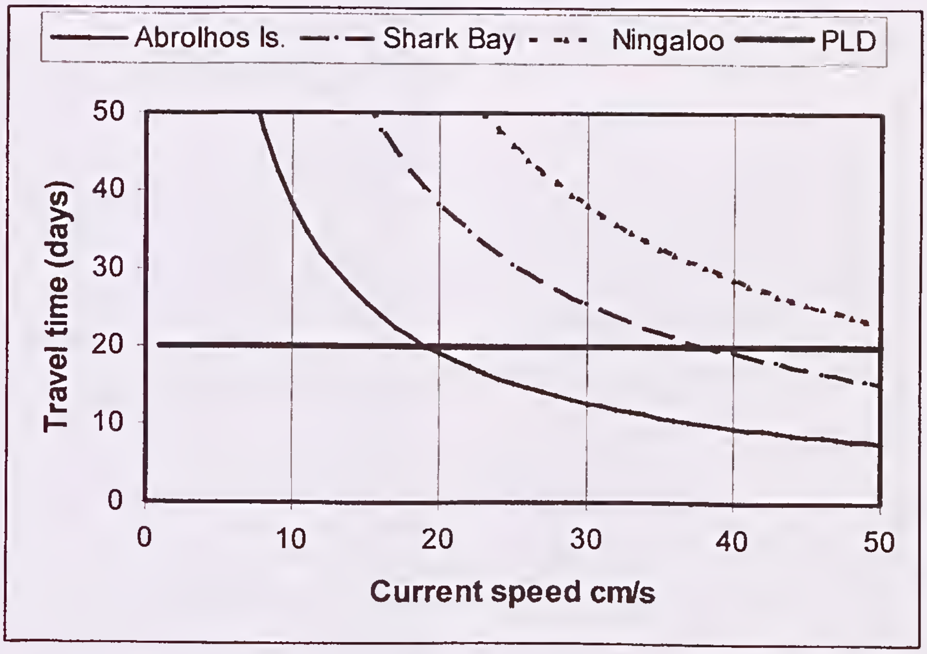

Figure 9. Speed/time relationship showing the time taken for planktonic larvae to reach Rottnest Island from the Abrolhos Islands (solid line), Shark Bay (dashed) and Ningaloo (dotted) at different mean current speeds. The pelagic larval duration of *Abudefduf* larvae has been set at 20 days (horizontal black line).

also noted the furthest southward travel of larvae in the 30-day period as an approximate indicator of the strength of the Leeuwin Current.

The results (not graphed here) clearly confirm that larvae could be carried well south of Rottnest Island by the Leeuwin Current – in some cases particles rounded Cape Leeuwin and were heading eastwards towards the Great Australian Bight within the month-long drift period. The results also indicate that larvae were widely dispersed offshore by the meander/eddy system and only a relatively small proportion of the original particles in fact passed anywhere near Rottnest Island. Adding to this the (unknown) larval mortality suggests that the likelihood of any particular larva dispersing from the Abrolhos Islands and recruiting at Rottnest is extremely small. Even though the Aus-Connie period 1995 to 1999 includes two of the peak recruitment years, the model did not reproduce the observed inter-annual abundances at Rottnest Island very well. This is almost certainly because of limitations of the simple processes incorporated into Aus-Connie (Condie *et al.* 2005) and also because of gaps in our knowledge of the biological attributes of the fish such as spawning strength, food availability and mortality.

Despite these limitations, modelling can provide a useful tool for comparing likely particle trajectories and hence the potential abundance of larval recruits at Rottnest Island over time. A finer resolution model with more flexible larval options (including swimming ability) is under development (Pearce *et al.* in prep.) and preliminary results confirm that larvae can be passively advected from the Abrolhos to Rottnest Island within 10 days (as suggested in Figure 9); many other larvae, however, will not arrive within their larval duration and so presumably perish. Even particles (larvae) released over successive 5-day intervals reveal a high level of variability in arrival times and abundance in the vicinity of Rottnest.

c) Cross-stream transport to the Island and local nearshore processes

Following their southward transport in the Leeuwin Current, the pelagic larvae are typically somewhere west of the continental shelf and need to reach the coastal waters of Rottnest Island by a combination of cross-shelf current/mixing processes, wind-driven surface currents (especially if the larvae are travelling under an algal raft), and active swimming. On finding suitable habitat, the larvae metamorphose to the juvenile stage and "settle" in the coastal reefs where they grow through the juvenile stage into adulthood, subject to suitable environmental conditions, adequate food, and predation.

Few current measurements have been made in the vicinity of Rottnest Island. Some early current observations (Cresswell *et al.* 1989) showed highly variable current patterns near Rottnest Island with occasional strong (20 to 30 cm/s) currents, while nearshore currents were generally much weaker: some measurements in Longreach Bay on the northern coast of the Island (Byrne 2001; Hopkin 2001) showed mean current speeds of < 5 cm/s with a peak of 17 cm/s. During each fish survey, the general flow of water in the vicinity of Pocillopora Reef was noted, showing that under typical southwesterly wind conditions warm offshore water flooded over the reef bringing in the new recruits, while with easterly winds cooler water from Porpoise Bay (to the northeast) displaced the warm water. It may be noted that, because of the micro-tidal range off the Perth coast, tidal currents in this area are negligible (Pearce *et al.* 2006a).

The wind regime off Rottnest Island in late summer (when the major *Abudefduf* recruitment tends to occur) is dominated by southerly winds modulated by the strong diurnal sea breezes (Masselink & Pattiaratchi 2001; Pearce *et al.* 2006a). These strong southerlies can result in an offshore near-surface Ekman transport of order 30 cm/s, overlying a weaker onshore current component (Muhling & Beckley 2007), so the vertical distribution of the larvae in the water column may govern whether they encounter onshore or offshore transport (Leis 2006), thus either assisting or hindering recruitment to the nearshore waters around Rottnest Island.

The wind would also directly affect drifting rafts of floating *Sargassum*, which can be packed with tiny fish (Hutchins 1995). These include both pre-settlement recruits as well as older larvae which have undergone metamorphosis and achieved full juvenile colouration under the raft. Some *Sargassum* rafts have been seen well west of Rottnest Island in the Leeuwin Current and can be quite extensive – on one occasion, a raft some 2 m wide and over a km long was seen 20 km west of Rottnest travelling south at 2 to 3 knots (BH). During the 1999 recruitment in particular, many large rafts of *Sargassum* washed into the bays along the south side of Rottnest and these were populated with small juveniles of tropical reef fish, including a number of category "b" *Abudefduf*'s. Over the years, many smaller patches of floating sargassum sampled near the south coast of Rottnest (Hutchins 1995) have in fact contained few or no *Abudefduf spp.*, so most of the *Abudefduf* recruits to Parker Point probably arrived as free swimming planktonic larvae.

There is little published information on the abundance, extent or seasonality of these algal rafts off the Western Australian coast. The possibility of marine larvae being transported down the coast under algal mats in the Leeuwin Current was suggested by Walker (1991), Dunlop (1997) and Dunlop & Rippey (1998) have reported Bridled Terns foraging over drift weed in coastal waters during late summer and early autumn. Fishers have also reported that such rafts or pontoons attract predatory fish (de Bruin 2007). The potential of drifting algal rafts to contribute to the dispersal of larval fish should be further investigated, both by direct observation/sampling and (for larger patches) using satellite remote sensing (Gower *et al.* 2006).

In addition to these oceanographic/meteorological processes which would passively transport planktonic larvae, late pre-settlement larvae are very competent swimmers. There is little direct information on the swimming capacity of our two *Abudefduf* species. Leis *et al.* (1996) directly observed the swimming behaviour of a number of coral reef larval fish (including one *A. sexfasciatus* and a second *A.* species), and suggested that "the faster fishes" were swimming at 20 to 30 cm/s, with the Pomacentrids being among the more competent swimmers. Experiments by Fisher *et al.* (2000) on *Pomacentrus ambionensis* confirmed that swimming ability increased with age/size, and was over 25 cm/s from an age of just 5 days after hatching. From an age of about 2 weeks, the larvae could swim 20 to 40 km over a period of up to 100 hours (*ibid.*). The growth rate and swimming endurance (and hence distance swum) of fish larvae can be greatly increased by active feeding during the swim (Leis & Clark 2005) so the food availability and type can be very important. While larval fish have been shown to swim directionally rather than at random (possibly following auditory and/or olfactory cues associated with the reef system – *e.g.*, Leis 2005), it is unclear whether they actively swim towards reef systems from some distance away or whether they passively encounter the reefs and then at close range seek out suitable settling habitat.

Based on the above, late stage *Abudefduf* larvae would have a likely swimming speed of about 10 to 20 cm/s, comparable with the ambient shelf currents which could therefore materially affect larvae either actively seeking or passively encountering the Island.

Water temperatures in February/March are at their summer peak of about 23 °C both offshore at Rottnest Island and near the coast at Marmion (Figure 1). These temperatures are maintained at Rottnest Island until about May (Figure 7b), before falling to about 19 °C in winter – these appear to be sufficient for the survival of newly-arrived *Abudefduf* larvae and juveniles, whereas any larvae near the coast would be unlikely to survive the nearshore winter temperatures of only 16 °C.

d) Inter-annual variability

The 2 major peaks in total *Abudefduf* abundance during the strong *La Nina* years 1999 and 2000 (Figure 5) were closely linked with the record high coastal sea levels and (larger-scale) surface temperatures in those years, and hence with an unusually strong Leeuwin Current (Figure 8). By contrast, the 1995 pulse in Figure 5 was at a time of relatively low sea level but this was also an anomalous year when the SST was high (Figure 8), suggesting that water temperature (rather than strong southward transport) may have contributed to the good recruitment that year by aiding rapid growth and survival. The lesser recruitment peak in 2001 (Figure 5) was during the fading stages of the 2000 *La Nina* when sea level was still elevated (Figure 8), but here the water temperature was marginally below average. Clearly, other (biological) factors also play an important role in recruitment, so successful recruitment requires both good larval supply and favourable environmental conditions.

Water temperature measurements in the continental shelf waters off south-western Australia have revealed a warming of about 1 °C over the past 5 decades (Pearce & Feng 2007). It is uncertain how this may directly affect recruitment at Rottnest Island, but there could well be a progressive southward range extension of tropical fish down the Western Australian coast. If water temperatures at Rottnest Island (present winter-to-summer range 19 to 23 °C – Figure 7b) were to approach those presently prevailing at the Abrolhos Islands (20 to 23.7 °C; Pearce 1997), it is possible that *Abudefduf* breeding populations could perhaps be sustained at the southerly location in the future.

Summary and Conclusions

Three decades of larval fish observations at Rottnest Island have shown the annual arrival of pulses of tropical fish larvae (two *Abudefduf* species have been examined here), most intensely in early autumn when water temperatures are still high and the Leeuwin Current is strengthening. The source of these larvae is almost certainly the Abrolhos Islands, and historical current measurements indicate that the Leeuwin Current is a more likely transport vector than the slower and more variable shelf currents. Recruitment is also possible from Shark Bay on occasion, and even (albeit rarely) Ningaloo Reef.

It is clear that both oceanographic and biological processes play very important roles in governing the seasonal and inter-annual levels of settlement. While we have shown that reasonable estimates of the ocean currents and their variability based on historical observations support the concept of southward inter-island transport, explaining the observed inter-annual fluctuations in settlement requires better knowledge of biological factors such as the larval abundance at the source (or spawning strength), and both mortality rates and food availability *en route*. Recent developments in hydrodynamic modelling of the current system are being undertaken to examine the dispersal/transport process in more detail, and the potential role of drifting rafts of *Sargassum* in the transport process also requires further investigation.

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Sea surface temperatures of the Leeuwin Current in the Capes region of Western Australia: potential effects on the marine biota of shallow reefs

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Abstract

The Leeuwin and Capes Currents have been shown to influence marine assemblages along the Western Australian coast. In this study we examined potential relationships between the sea surface water temperature (SST), as a consequence of the Leeuwin and Capes Currents, and the distribution of fishes and algae. Data were collected from locations that spanned the temperate Capes coast (33°30' to 34°25'S). Fish assemblages were measured using diver operated stereo-video and stereo baited remote underwater video. Algae were harvested from quadrats. Mean SST at the most southerly region was 18.5°C while regions on the west coast of the Capes were generally one degree warmer.

Seventy three species of fishes were recorded belonging to 36 families. Two species were classified as tropical and one species as sub-tropical (*Cirrhilabrus temmincki, Plectorhinchus flavomaculatus* and *Choerodon rubescens* respectively). Forty four percent of species from the Capes were classified as either tropical, subtropical or subtropical-temperate. The remainder were of temperate or widespread distributions.

Two hundred and five species of algae were recorded belonging to 49 families. All species were regarded as temperate with the exception of the geniculate red alga, *Rhodopeltis borealis.* Eleven range extensions were recorded for algae: two were southward of the current known range (*Champia compressa* and *Rhodopeltis borealis*) and the remaining nine were northward or westward extensions.

Within the 120 km of the Capes coast studied, regions with warmer waters did not have higher abundances of fishes of tropical, subtropical or subtropical-temperate origin than cooler waters. However, the most southerly region was different in terms of algal assemblage structure with water temperature the most influential of environmental variables, relative to exposure, substratum and depth.

The large proportion of fish species with tropical, subtropical and particularly subtropical-temperate distributions recorded is consistent with other studies and may be due to the influence of the Leeuwin Current. The range extensions for algal species may be due to the effects of the Leeuwin and Capes Currents but may also be due to the paucity of algal collections from some parts of the Capes region. Other factors such as topographic complexity, depth and other habitat structure variables may also be influencing marine assemblages. The findings of the work support the notion that there is a large transition zone between biogeographic provinces within which the Capes region is positioned.

Keywords: Leeuwin current, Western Australia, Capes, fishes, algae, reefs, water temperature

Introduction

Oceanic currents have the potential to influence dispersal and distribution of marine species (McGilliard & Hilborn 2008) sometimes across thousands of kilometres (Shanks *et al.* 2003). The Leeuwin Current (LC), which originates in the tropics, carries warmer waters southwards past the coastline of Western Australia and has been shown to influence the distribution of fishes (Hutchins 1991; Ayvazian & Hyndes 1995), corals (Hatcher 1991), lobster (Caputi *et al.* 1996) seagrasses and algae (Walker 1991). A consequence of the LC is that the marine biotic assemblages of south western Australia contain species that extend further southward in their range than would otherwise be possible. Although the poleward moving LC is dominant along the west coast, it is met by the Capes Current (CC), a cool equatorward counter current near the south west corner of Western Australia (Pearce & Pattiaratchi 1999) that may also influence the distribution of marine biota.

We propose that the unusual oceanographic conditions in the Capes region (Busselton to Augusta) Western Australia, which result from the combined effects of the LC and the CC, influence the distribution of marine flora and fauna. We compare distributions of fishes and algae that were recorded in the Capes region, to known distributions to assess the proportions that are regarded as more tropical in their range. We also investigate variations in the distribution of species within the Capes region that may be due to these currents. The paper forms part of a larger study to establish a benchmark of data on fishes and algae in the Capes region, and to assess changes in these over time in proposed, and then gazetted, sanctuary zones. Consequently the design, the location of sites and the data collection methods were predefined as part of the broader project.

This paper provides: a summary of the information on the Leeuwin and Capes Currents in the Capes region (more detailed accounts are provided elsewhere in this special issue) and how they may influence marine biota; a description of other factors that may influence the structure of marine biota in the Capes region; a summary of some previous investigations of marine biota, the influence of the LC and how these relate to the Capes region; and an examination of relationships between sea surface temperatures, as a consequence of the LC and CC, and marine biota in the Capes region of Western Australia from a comprehensive survey of reef communities.

The Leeuwin and Capes Currents

The LC is unusual as unlike other eastern boundary currents, it transports warm tropical waters polewards, and simultaneously inhibits upwelling (Pearce 1991). It flows from Exmouth, Western Australia, past Cape Leeuwin and on to the Great Australian Bight (Maxwell & Cresswell 1981; Cresswell & Peterson 1993; CSIRO 2001) with an influence as far as Tasmania (Ridgway & Condie 2004). The waters are low salinity (Cresswell & Peterson 1993) and relatively nutrient poor (Pattiaratchi 2006). The LC is narrow (< 100 km wide) and shallow (< 300 m deep) (Pattiaratchi 2006) by global standards for a major current system and flows at a relatively high velocity (0.1–1.0 ms^{-1}) (Smith *et al.* 1991; Cresswell & Peterson 1993). It is seasonal, with higher flow during autumn, winter and early spring than in summer (Pearce 1991) and with fluctuations in the rate of flow linked to variations in wind stress (Godfrey & Ridgway 1985; Smith *et al.* 1991). The southerly flow of the current changes direction at Cape Leeuwin, turning east and then continuing into the Great Australian Bight. Downwelling of the LC results in low nutrients and consequently low levels of primary production (Hanson *et al.* 2005; Pattiaratchi 2006) which in turn influences fisheries (Gaughan 2007).

The CC is a wind-driven, high salinity, cool water current that flows equatorward, is strongest from Cape Leeuwin to Cape Naturaliste, and widens to extend northwards beyond Perth (Pearce & Pattiaratchi 1999). In summer, the LC is met in the Capes region by waters of the CC, which occupy most of the continental shelf and consequently inhibit the flow of the LC across the shelf (Cresswell 1991; Pearce & Pattiaratchi 1999; CSIRO 2001). In the winter months, the CC does not flow, allowing the LC to flood across the continental shelf to the coast to warm the inshore waters. The shallow waters in Geographe Bay, however, remain cool due to loss of heat to the atmosphere (CSIRO 2001). Due to the presence of the CC, oceanic waters of the Capes region undergo a different seasonal regime compared to other waters influenced by the LC.

Water temperatures at Cape Mentelle, in the central part of the Capes region, range from approximately 21°C in March / April to 17.5°C in September (Pearce & Pattiaratchi 1999). The peak temperatures are associated with a weakening of the CC. The water temperature range at Cape Mentelle, of approximately 4°C, is less than the 7°C range in the Perth region (Pearce & Pattiaratchi 1999).

The LC has been shown to influence marine biota by providing warmer waters for more tropical species (Gopurenko *et al.* 2003; Hutchins 1991; Maxwell & Cresswell 1981); lowering temperature range on inshore reefs as has been shown at Cape Mentelle (Pearce & Pattiaratchi 1999); and transporting the larvae or adults of various species (Caputi *et al.* 1996). In contrast the CC influences the region by transporting cooler waters from the south and associated marine species (Pearce & Pattiaratchi 1999), although the influence of the CC may be less than the LC as it is not the dominant current and flows only in the summer.

Other factors that structure marine reef communities of the Capes region

The structure of marine reef communities is influenced by many factors in addition to currents, such as wave energy and exposure, depth, substratum type and topographic complexity (rugosity or vertical relief of reefs). Any investigations into the effect of currents and water temperature on marine biota should also consider these smaller scale influences.

Cape Naturaliste, in the north of the Capes region, has been described as being a high energy region, when compared with other exposed regions on the Australian coast, with high flow bed shear stresses due to the LC and storm impacts from the South West (Hemer 2006). High shear stresses would likely influence the recruitment and growth of benthic macroalgae and associated fish communities.

The Capes region is dominated by limestone and granite reefs of varying depths, levels of topographic complexity and wave exposure. Kendrick *et al.* (2004) showed that variation in the macroalgal assemblages in the Capes region was driven by whether the substratum was limestone or granite, depth was <10 m or 10–20 m, and whether the reef was high relief (> 2 m), or low relief. A study by Toohey (2007) in the Hamelin Bay region of the Capes showed that algal assemblages were structured by different levels of topographic complexity, which influenced light, water motion and sediment cover. Also at Hamelin Bay, Harman *et al.* (2003)

recorded differences in fish assemblages between limestone and granite reefs, and between high and low relief reefs. High relief reefs had larger numbers of fish species than low relief reefs. The kelp *Ecklonia radiata* was more dominant on low relief limestone reefs but was less dominant on granite reefs and high relief limestone reefs. Ayvazian & Hyndes (1995) noted that surf zone fish assemblages in the Capes region were influenced by the presence of seagrasses or patch reefs.

Differences among regions in the current study, or larger scale differences in marine biota that may be attributable to the Leeuwin and Capes Currents, would also very likely be influenced by the aforementioned, and other, structuring processes.

Previous studies of marine biota and the influence of the Leeuwin and Capes Currents

The LC has been shown to influence the distribution of fishes and nearshore fisheries along the Western Australian coast (Lenanton *et al.* 1991). Ayvazian & Hyndes (1995) noted an influence of the LC on surf zone fish assemblages. Lower numbers of species on the south coast and an absence of tropical species were attributed to the reduced influence of the LC compared with the west coast.

Strengthening of the LC flow in March coincides with recruitment of tropical fish species at Rottnest Island (Hutchins & Pearce 1994) which, at a latitude of 32°S, is a temperate marine environment and is approximately 200 km north of the Capes region. Hutchins (1991) recorded an autumn / winter influx of juvenile tropical fishes at Rottnest Island in areas that are influenced by the LC. The most likely source of breeding stocks was thought to be the Houtman Abrolhos Islands 350 km to the north and larval durations of the species observed were sufficient to cover this distance at the LC rate of 2 to 3 knots. Approximately 17% of reef associated nearshore species were classified as tropical.

Gopurenko *et al.* (2003) recorded mud crabs (Portunidae; *Scylla* spp.) in SW Australian estuaries 1000 km south of their recorded distribution and linked this to a recruitment event enhanced by the strong 1999/2000 LC.

A number of studies have investigated the influence of the LC on commercially important fisheries. Low levels of finfish production in the region are primarily due to the low nutrient waters of the LC (Caputi *et al.* 1996). However, the LC has a positive influence on post larval settlement of the western rock lobster (*Panulirus cygnus*) (Phillips *et al.* 1991). When the LC is strong the settlement of puerulus generally occurs 2° further south than in years when the LC is weak (Caputi 2008).

The influence of the LC on finfish is not consistent among species. It has been shown to have a negative effect on larval survival of pilchards (*Sardinops sagax neopilchardus*) but a positive impact for whitebait (*Hyperlophus vittatus*) (Lenanton *et al.* 1991; Caputi *et al.* 1996; CSIRO 2001). In contrast it has been suggested that the CC influences the commercial salmon fishery in the SW region by providing a conduit of cooler water that allows them to migrate around Cape Leeuwin and up the west coast (Pearce *et al.* 1996). Gaughan *et al.* (2007) suggested that the LC system most likely contributes a net negative impact on success of teleost eggs and larvae on the west coast of Australia. Larvae are likely to be trapped in warm core eddies that form from the LC and would contribute little to nearshore recruitment.

Some tropical species of coral that are able to tolerate cooler conditions form isolated colonies in the Capes region, including species of the massive corals *Favites*, *Goniastrea* and *Turbinaria* (Veron 2000; Veron & Marsh 1988). Fourteen species of coral from seven genera were previously recorded in seagrass beds and among small macroalgae in Geographe Bay in the Capes region (Veron & Marsh 1988).

Patterns of algal distribution are the result of dispersal, settlement and recruitment, and growth, (Walker 1991) and the LC may affect any or all of these processes. Effects of the LC on the marine flora are less detectable, however, than those on the fauna and may be due to limited habitat availability and/or limited dispersal distances of algae (Walker 1991). In their study of the algae of Rottnest Island, Huisman & Walker (1990) found that most species were of temperate affinity and only sporadic occurrences of 'tropical' species were recorded, which suggests that water temperature is important. They suggested that the variable strength of the LC could account for the relatively few 'tropical' algae at Rottnest Island (Huisman & Walker 1990).

Drift algae have greater dispersal potential than species that rely solely on spore dispersal. Species of *Sargassum*, for example, are often positively buoyant once detached from the substrate and viable plants could be transported into suitable habitats on the south coast by the LC (Phillips 2001). Walker (1991) suggested that the presence of *Sargassum decurrens* at Rottnest Island may be the result of the southerly flowing LC, as this species has a northerly distribution in Australia.

When kelp-associated algal distributions were examined over a wide geographic area, Wernberg *et al.* (2003) found that distinct regional algal assemblages could be discriminated, with some overlap between adjacent regions. While regional differences were evident, it was found that local- and small-scale processes also contributed significantly to kelp-associated algal assemblages (Wernberg *et al.* 2003). The kelp *Ecklonia radiata* decreased in importance as a canopy species moving south, and may be the result of decreasing water temperature (Wernberg *et al.* 2003 and references therein).

The oceanographic conditions in the Capes region due to the LC and the CC may therefore influence the marine biota of nearshore reefs and, based on the findings of previous studies, water temperature and larval transport are the factors most likely to influence these biota (Lenanton *et al.* 1991; Phillips *et al.* 1991; Walker 1991;Caputi *et al.* 1996; Gopurenko *et al.* 2003). However other factors such as depth, exposure and substratum type will play a part in structuring the marine communities. This paper uses data from a benchmark study on nearshore marine reef communities of the Capes region to investigate the potential influence of the LC on fish and algal assemblages of shallow reefs (10 to 20 m). Specifically: the distributions of species are compared with known broadscale distributions; and then relationships are tested between biological (the composition of fish and algal assemblages) and physical variables (water temperature, substratum type, depth and exposure) at a regional scale within the Capes.

Methods

Site selection

The data used in this paper form part of a larger study in the Capes region to set marine benchmarks and to evaluate the effect of sanctuary (no-take) zones on marine reef assemblages. Four regions from that study were included in the current paper with the aim of examining the effect of the LC. These were Naturaliste, Freycinet, Hamelin and Flinders Bay; with four sites at each region (Figure 1) that span 120 km of coast from 33°30' to 34°25'S. Data were collected in summer of 2005–06.

Reef sites were selected to be representative of the broader habitat types within a region so that results could be used to predict the nature of surrounding reef areas. Sites were selected using aerial photography, nautical charts, and habitat maps and were verified in the field using a cable mounted video camera. A depth sounder was used to examine the relief or roughness of the seafloor and sampling was then done using SCUBA. Sites within the Flinders and Hamelin regions were approximately 8 to 11 m deep and sites in the Naturaliste and Freycinet regions were 15 to 18 m deep.

Algae

Algae were collected from quadrats of 0.5 x 0.5 m (0.25 m^2) (n = 6 nested within 4 locations in each region) that were randomly stratified on reef. All algae in the quadrat were harvested, sorted to species and wet weighed to determine the composition (number of species and their weight). Algae were identified by experienced algal taxonomists/ecologists (Drs. John Huisman, Julia Phillips and Gary Kendrick) with reference to standard algal identification guides (*e.g.*, Womersley 1984, 1987, 1994, 1996, 1998, 2003). Selected voucher specimens were lodged with the Western Australian Herbarium.

Fishes

Censuses of fishes were done using diver operated stereo videography (DOV). This involves using an underwater stereo-video system comprised of two forward facing video units secured to an aluminium frame (Harvey *et al.* 2001; 2002a). A light emitting diode,

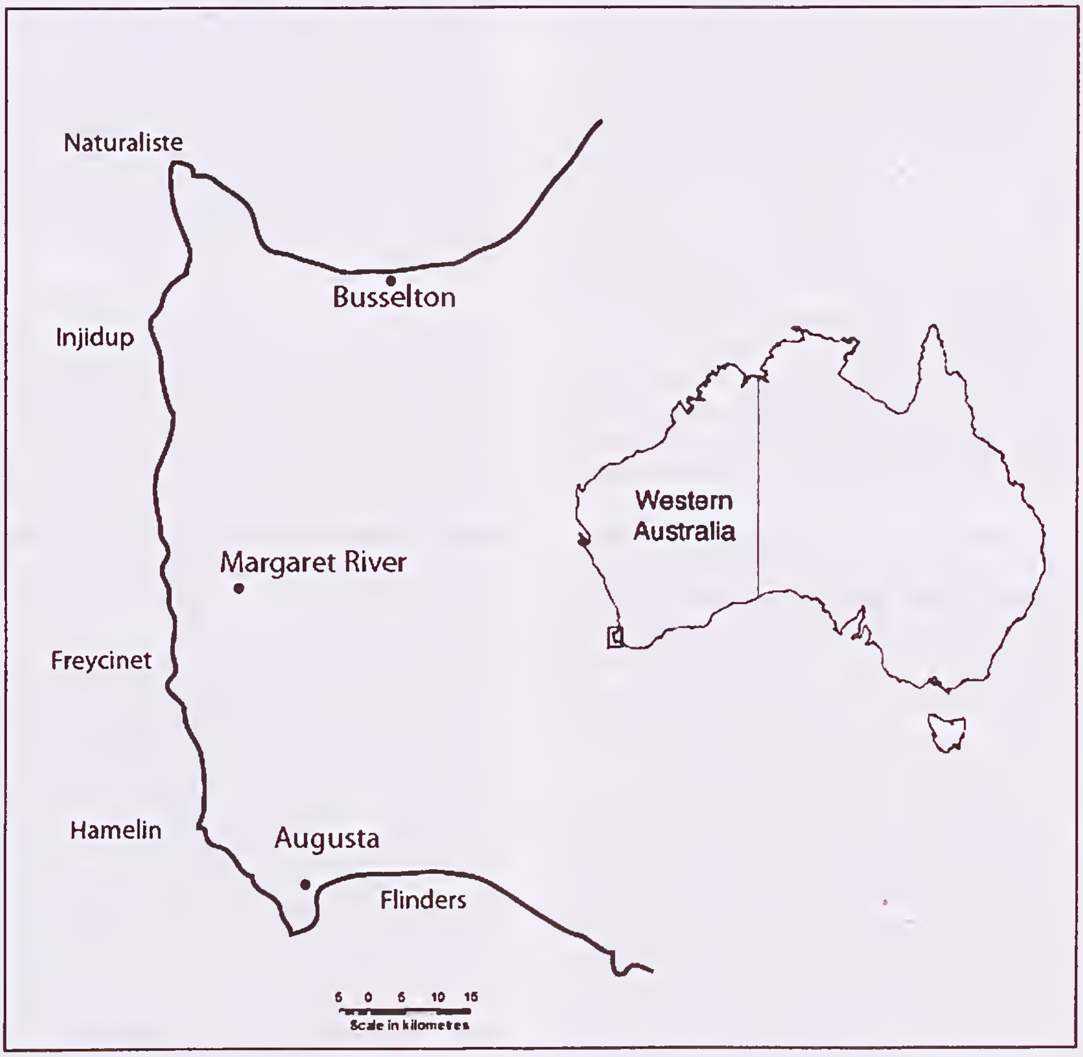

Figure 1. Western Australia and the site locations from this study: Naturaliste, Freycinet, Hamelin and Flinders.

positioned on a rod in front of the cameras, enables the footage to be synchronised when it is viewed on computer. The video units are configured to record the fish from different angles and a computer program is then used to calculate the size of fishes by mathematical triangulation using the two sets of video footage. The video units were swum along replicate underwater transects (75 m long x 5 m high x 5 m wide) by SCUBA divers, and the number of fish per unit area was calculated (n = 4 nested within 4 locations in each region). The transect size was determined from tests that showed high variability at some sites due to low numbers of fishes. Recordings were post processed to identify, count and measure the fork lengths (length from the head to the fork of the tail) of all reef fish seen. Sampling was conducted between 08:00 and 16:00 hours when water visibility was greater than 5 m. The stereo-video system does not fully sample small cryptic fishes, which are most effectively sampled by icthyocides (poisons that kill fish) (Ackerman & Bellwood 2002). This study focuses on non-cryptic reef fish species longer than 40 mm.

The use of stereo video enables conclusive identification of species from the video footage and tests have shown the accuracy of size estimates to be within 2 mm (Harvey *et al.* 2003). Video footage can be stored for long-term comparisons or re-analysis and there is also no bias from different observers who might incorrectly identify fishes of similar species or appearance when underwater.

Censuses of fishes were also undertaken using stereo baited remote underwater video (stereo-BRUV) (Harvey *et al.* 2002b). This method utilises stereo-video units similar to those used for diver operated stereo-video (DOV), however BRUVs were attached to a frame and lowered to the seafloor with a sealed bag of bait in front of the cameras. Video footage was collected to determine the number and size of fishes that visit or inspect the bait. The maximum number of species *i* at any time *t* (*MaxNi,t*) was recorded from viewing 45 min duration of footage, and used as a measure of relative abundance between sites. Stereo-BRUV of fishes was conducted at the Cape Naturalise and Injidup regions (Figure 1). For this paper the stereo-BRUV data were specifically used to examine species ranges and compare with documented distributions.

Temperature, substratum, exposure and depth

Water temperature data were sourced from the National Oceanic and Atmospheric Administration (NOAA) and National Aeronautics and Space Administration (NASA) (2007). These data were derived from the jointly developed AVHRR program where Advanced Very High Resolution Radiometer satellites were deployed to record accurate sea surface temperatures. Coordinates from the AVHRR dataset were selected on the basis of being in close proximity to the study sites and spanned five years, from 2002 to 2006 inclusive. These temperature data provided the study with information on spatial variation in temperature among the four regions. More information on this procedure can be found in Smith (1996).

The NOAA data are sea surface temperatures and water temperature may change with depth. However, Pearce (1997) stated that vertical mixing usually ensures that the temperature of the surface is close to the temperature of the upper few metres of water and generally reflects the subsurface thermal structure. Hemer (2006) described Cape Naturaliste as one the highest energy locations in Australia due to shear bed stress, the LC and storm activity. The region is also subject to average winds of greater than 20 km/h (Bureau of Meteorology, 2008) for every month of the year. These factors would likely provide sufficient mixing of the surface layer to the depths of our sites (< 20 m) such that sea surface temperature data could be assumed to closely represent the water column temperature structure.

Substratum was classified as belonging to one of the following three categories: limestone, granite or a combination of limestone and granite based on observations at the sampling locations and habitat maps (Department of Environment and Conservation, 2006). Exposure of the sites to wave energy was defined as either low, medium or high. This was based on data obtained from Geoscience Australia (2005) and from observations in the field. Water depth was measured in metres.

Patterns of distribution

Broadscale (Western Australia) patterns of distribution of fishes and algae were investigated using known ranges of species and applying these to the species recorded in our surveys. It was inferred that species with tropical or subtropical distributions might not be expected at these latitudes in the absence of the warm LC.

Data on the distributions of fishes were taken from Fishbase (Froese & Pauly 2008), Kuiter (1996), Hutchins & Swainston (2006) and Allen (1997). Fish species were regarded as tropical, subtropical, subtropical-temperate, temperate or widespread (*i.e.*, recorded in a range of climates or widespread across the Indo-Pacific region).

Data on algal distributions were taken from Algaebase (Guiry & Guiry 2008), Womersley (1984, 1987, 1994, 1996, 1998, 2003), Huisman (2000), Huisman & Borowitzka (2003), and Goldberg & Kendrick (2005).

Occurrences of species outside their documented range were also noted and regarded as range extensions or new records for the Capes region. These were determined by comparing our records with the scientific literature and databases.

Regional scale patterns of distribution were examined (*i.e.*, among regions within the Capes) to investigate whether there were differences in species composition of fishes or algae among the regions sampled (Naturaliste, Freycinet, Hamelin and Flinders).

Analyses

Data were analysed using Primer 6 (PRIMER-E Ltd, 2005) to explore trends in the fish and algal assemblages, and relationships with the aforementioned environmental variables; water temperature, mean water depth, substratum type and exposure at each region. A Bray-Curtis dissimilarity matrix was produced using square root transformed data, followed by non-metric multi-dimensional scaling ordination (nMDS) to investigate trends in the composition of fish and algal assemblages. These were overlain with vectors that were based on the correlation between the environmental and the ordination scores and allowed us to infer the degree of influence over the biological data. Pearson correlation coefficients were produced to explore the strength of any observed relationships (Clarke 1993; Clarke & Gorley 2006). Species level data were used to make inferences regarding range distributions and extensions for algal and fish species in the region. ANOSIM (Clarke & Warwick 1994) was used to determine the significance of any clustering of replicates, within regions, in nMDS ordinations.

Results are presented as broadscale patterns of distribution (*i.e.*, the influence of the LC and CC on the Capes region in general) and regional patterns (*i.e.*, an investigation of differences among regions within the Capes region – Naturaliste, Freycinet, Hamelin and Flinders).

Results

Water temperature

Flinders Bay was the most southerly region and had the lowest mean sea water temperature over the five years (18.5°C). In 2004 it was the lowest of all measures at all regions (17.7°C). Mean sea water temperatures were, however, similar among the Naturaliste, Freycinet and Hamelin regions (19.7°C, 19.43°C and 19.4°C

Table 1

Fish species recorded at the Capes using DOV and stereo-BRUV and their distributions (widespread, tropical, subtropical, subtropical temperate, and temperate) based on (Kuiter 1996; Hutchins & Swainston 2006; Froese & Pauly 2008).

Family	Species	Family	Species
Widespread		**Temperate**	
Aracanidae	*Anoplocapros lenticularis*	Caesioscorpididae	*Caesioscorpis theagenes*
Berycidae	*Centroberyx lineatus*	Cheilodactylidae	*Dactylophora nigricans*
Carangidae	*Pseudocaranx dentex*	Cheilodactylidae	*Nemadactylus valenciennesi*
Heterodontidae	*Heterodontus portusjacksoni*	Dasyatidae	*Dasyatis brevicaudatus*
Kyphosidae	*Kyphosus cornelii*	Dinolestidae	*Dinolestes lewini*
Sillaginidae	*Sillago ciliata*	Enoplosidae	*Enoplosus armatus*
Sparidae	*Chrysophrys auratus*	Gerreidae	*Parequula melbournensis*
Sphyraenidae	*Sphyraena novaehollandiae*	Glaucosomidae	*Glaucosoma hebraicum*
Tropical		Kyphosidae	*Kyphosus sydneyanus*
Haemulidae	*Plectorhinchus flavomaculatus*	Labridae	*Achoerodus gouldii*
Labridae	*Cirrhilabrus temmincki*	Labridae	*Austrolabrus maculatus*
Sub-tropical		Labridae	*Bodianus frenchii*
Labridae	*Choerodon rubescens*	Labridae	*Dotalabrus aurantiacus*
Labridae	*Halichoeres brownfieldi*	Labridae	*Pictilabrus laticlavius*
Sub-tropical – temperate		Labridae	*Pseudolabrus biserialis*
Aplodactylidae	*Aplodactylus westralis*	Monacanthidae	*Meuschenia flavolineata*
Aulopidae	*Aulopus purpurissatus*	Monacanthidae	*Meuschenia freycineti*
Berycidae	*Centroberyx gerrardi*	Monacanthidae	*Meuschenia hippocrepis*
Carangidae	*Seriola hippos*	Muraenidae	*Gymnothorax prasinus*
Chaetodontidae	*Chelmonops curiosus*	Muraenidae	*Gymnothorax woodwardi*
Girellidae	*Girella tephraeops*	Odacidae	*Odax acroptilus*
Girellidae	*Girella zebra*	Odacidae	*Odax cyanomelas*
Labridae	*Coris auricularis*	Odacidae	*Siphonognathus beddomei*
Labridae	*Notolabrus parilus*	Pempherididae	*Pempheris multiradiata*
Labridae	*Ophthalmolepis lineolatus*	Plesiopidae	*Trachinops noarlungae*
Monacanthidae	*Meuschenia galii*	Pomacentridae	*Parma victoriae*
Monacanthidae	*Meuschenia venusta*	Rhinobatidae	*Trygonorrhina fasciata*
Mullidae	*Upeneichthys vlamingii*	Scorpididae	*Scorpis aequipinnis*
Myliobatidae	*Myliobatis australis*	Serranidae	*Acanthistius serratus*
Orectolobidae	*Orectolobus hutchinsi*	Serranidae	*Caesioperca rasor*
Pempherididae	*Pempheris klunzingeri*	Serranidae	*Epinephelides armatus*
Platycephalidae	*Platycephalus speculator*	Urolophidae	*Urolophus mucosus*
Plesiopidae	*Paraplesiops meleagris*	Urolophidae	*Urolophus circularis*
Pomacentridae	*Chromis klunzingeri*		
Pomacentridae	*Parma mccullochi*		
Scorpaenidae	*Neosebastes pandus*		
Scorpididae	*Neatypus obliquus*		
Scorpididae	*Scorpis georgianus*		
Scorpididae	*Tilodon sexfasciatum*		
Scyliorhinidae	*Aulohalaelurus labiosus*		
Serranidae	*Callanthias australis*		
Serranidae	*Othos dentex*		
Urolophidae	*Trygonoptera ovalis*		

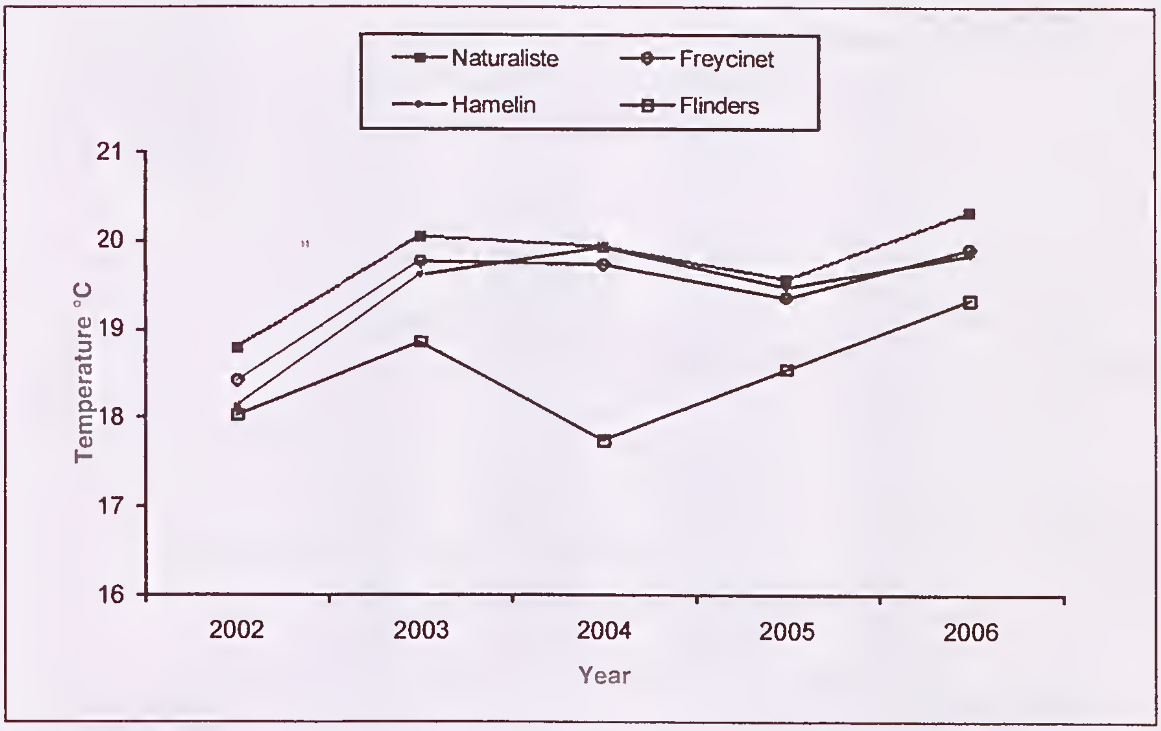

Figure 2. Sea water temperatures from NOAA data (NASA, 2007).

respectively) (Figure 2). The highest annual mean temperature was 20.3°C at Cape Naturaliste in 2006.

Broadscale patterns of distribution

We recorded 73 species of fishes from the DOV and stereo-BRUV throughout the Capes region which belonged to 36 families (Table 1). Based on the distributional classifications (Allen 1997; Froese & Pauly 2008; Hutchins & Swainston 2006; Kuiter 1996) two tropical and one sub-tropical species were recorded. Respectively these were: *Cirrhilabrus temmincki* (Peacock wrasse), *Plectorhinchus flavomaculatus* (gold spotted sweetlips) and *Choerodon rubescens* (baldchin groper). Twenty nine species were regarded as subtropical-temperate, 33 species as temperate and 8 species as widespread (Figure 3).

Cirrhilabrus temmincki is a tropical labrid species that inhabits outer coral reefs (Allen 1997) in waters of 23 to 28° C and is distributed from Japan to the Philippines and northern Australia (Randall 1992). The furthest southern recording is from the Abrolhos Islands (Allen 1997). This species was recorded at Injidup, which is

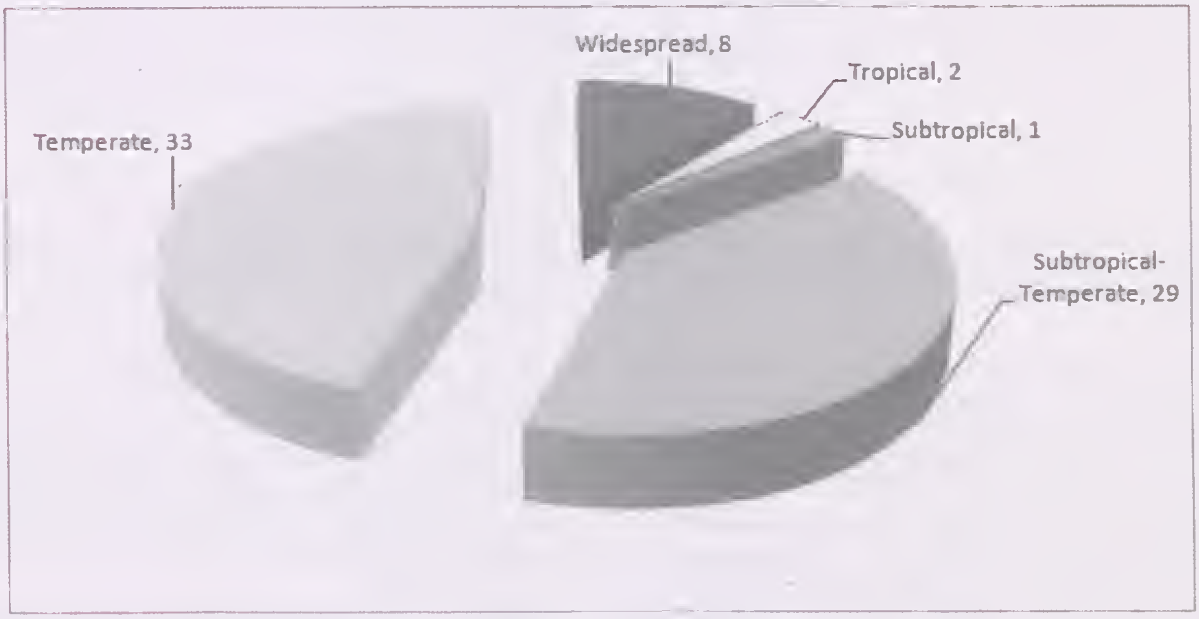

Figure 3. Distributional classification of all fishes recorded in the Capes region using DOV and stereo-BRUV.

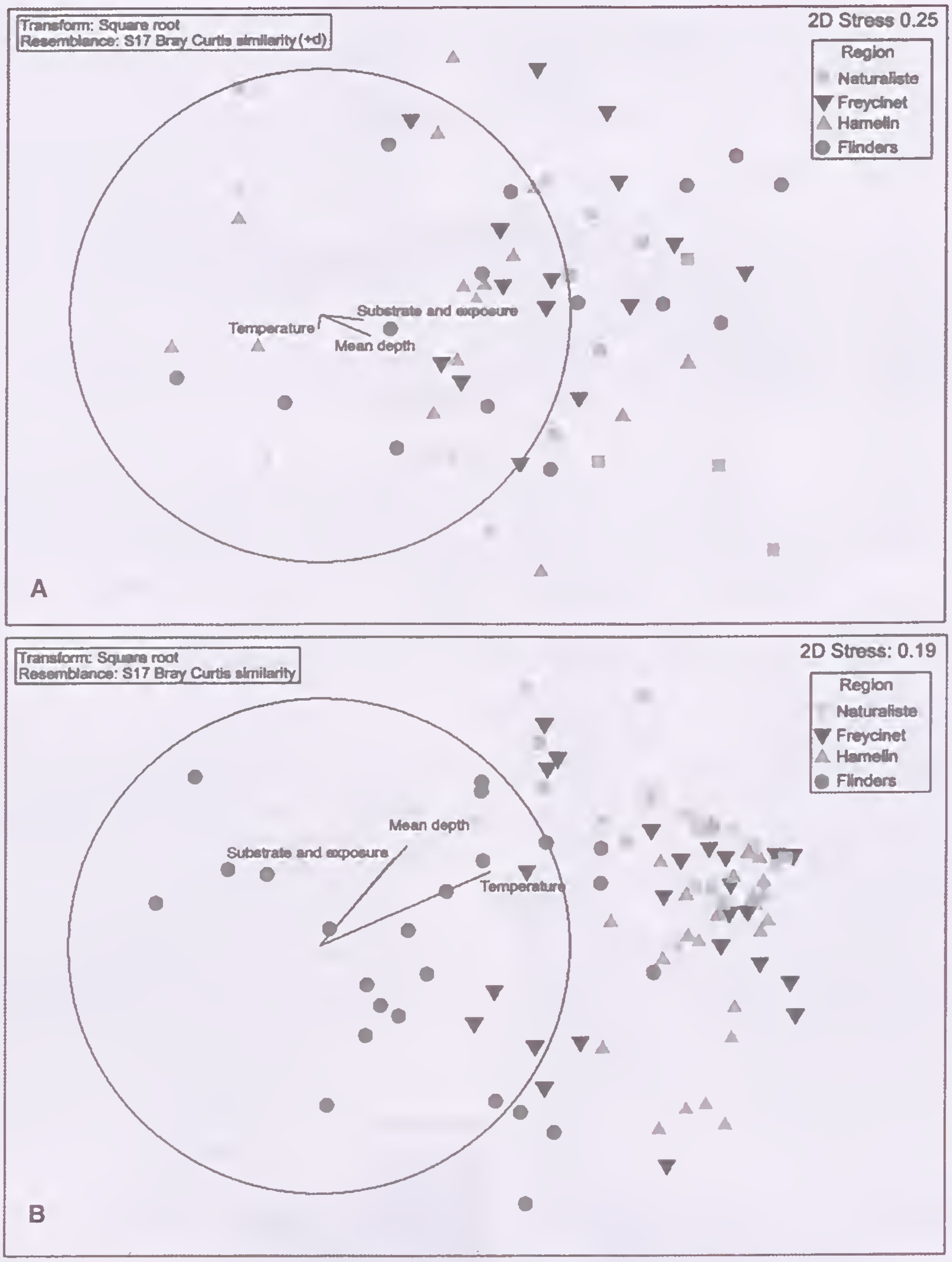

Figure 4. NMDS ordinations based on (A) fish assemblage and (B) algal assemblage structure for each of the sites. Similarity in assemblage composition is represented by the distance between each of the points. Vectors represent each of the environmental variables examined (mean depth, exposure, water temperature and substratum).

approximately 550 km south of the Abrolhos Islands. *Plectorhinchus flavomaculatus* is a tropical species inhabiting coral reefs but is occasionally reported in more southern waters such as Geographe Bay (Hutchins & Swainston 2006) and was recorded at Injidup.

Choerodon rubescens inhabits coral reefs and is occasionally found in the deeper offshore reefs along the lower west coast of WA, with a documented range from Geographe Bay to Coral Bay (Hutchins & Swainston 2006). We recorded this species south of Geographe Bay in stereo-BRUV sampling near Sugarloaf Rock (Cape Naturaliste) and at Injidup.

A total of 205 algal species were recorded in the Capes region, belonging to 49 families. Red algae (Rhodophyta) were the most speciose and accounted for around 68% of all species. Brown (Heterokontophyta) and green (Chlorophyta) algae made up approximately 22% and 10%, respectively.

In terms of biogeographic affinity, all species can be regarded as temperate with the exception of the

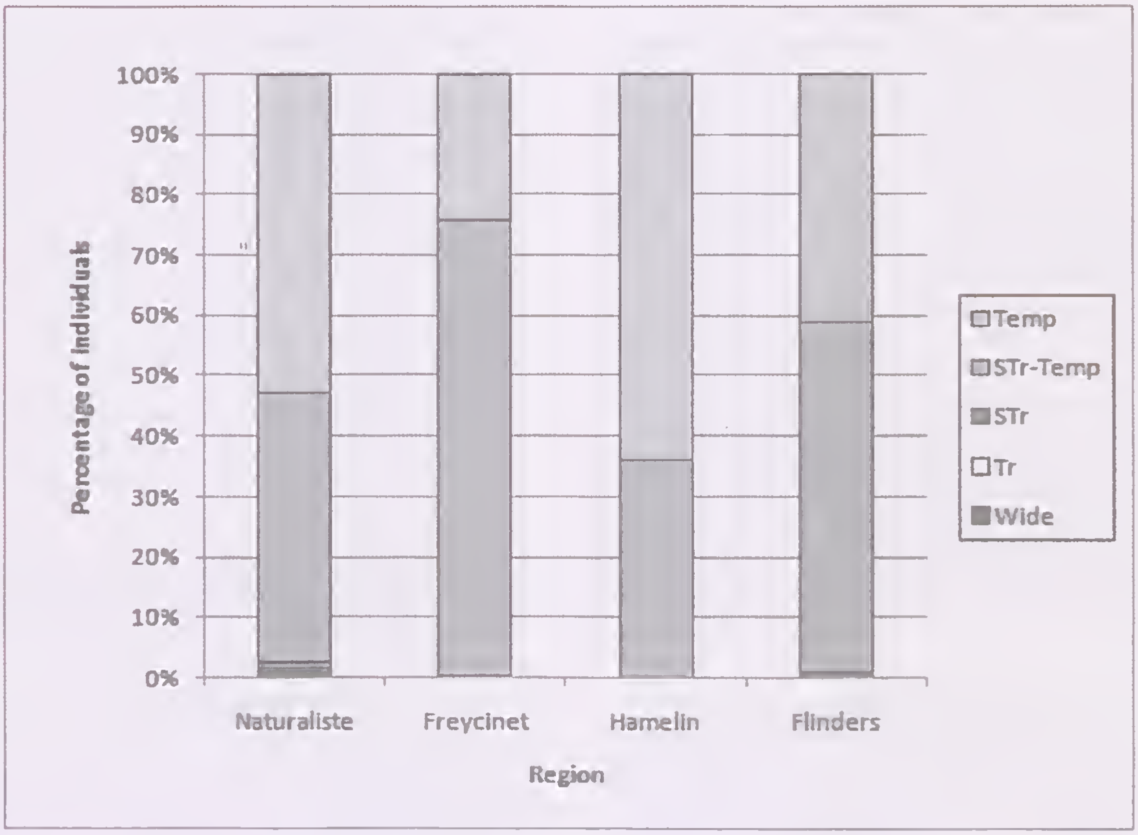

Figure 5. The proportion of fishes in each distributional classification at each region of the Capes. Notes: categories based on (Froese & Pauly 2008; Hutchins & Swainston 2006; Kuiter 1996); Temp – temperate; STr-Temp – subtropical temperate; STr – subtropical; Tr – tropical; Wide – widespread; and tropical sub-tropical species were only recorded at Naturaliste (each 0.3%).

geniculate red alga, *Rhodopeltis borealis*. For this reason, we instead relied on apparent range extensions to provide insight into broadscale patterns of distribution.

Eleven range extensions for algae were recorded during this study. Two of these are southward extensions of the current known range of particular species; the remaining nine are northward or westward extensions (Table 2). *Champia compressa* and *Rhodopeltis borealis* have previously been recorded as far south as Rottnest Island (Huisman 2000), but in this study were found as far south as Flinders Bay and Cape Freycinet, respectively. Northward and/or westward range extensions varied in the distance over which the known range has been extended by this study. *Alleynea bicornis* and *Echinothamnion hookeri*, for example, were previously known as far east as Albany on the southern WA coast (Womersley 2003). Published records for *Codium dimorphum* in Australia are restricted to Tasmania (Womersley 1984); in this study it was found in the Flinders Bay region.

Table 2

Algal range extension (new records) from algal collections in the Capes region.

Range extension	Algal species	Division	Family
Southward	*Champia compressa*	Chlorophyta	Codiaceae
	Rhodopeltis borealis	Rhodophyta	Dumontiaceae
Northward / westward	*Alleynea bicornis*	Rhodophyta	Rhodomelaceae
	Codium dimorphum	Chlorophyta	Codiaceae
	Echinothamnion hookeri	Rhodophyta	Rhodomelaceae
	Mychodea australis	Rhodophyta	Mychodeaceae
	Phyllospora comosa	Heterokontophyta	Seirococcaceae
	Sargassum paradoxum	Heterokontophyta	Sargassaceae
	Sargassum vestitum	Heterokontophyta	Sargassaceae
	Thuretia australasica	Rhodophyta	Dasyaceae
	Zonaria angustata	Heterokontophyta	Dictyotaceae

Regional scale patterns of distribution

There were no obvious patterns in the fish assemblage structure among the four regions (Naturaliste, Freycinet, Hamelin and Flinders) in nMDS ordinations and this was supported by a non-significant ANOSIM result (R – value 0.014, sig 25%). Water depth was the most influential of environmental variables on species composition, rather than water temperature, exposure or substratum (Figure 4). Regions with warmer waters did not have higher abundances of fishes of tropical, subtropical or subtropical-temperate origin (Figure 5).

There was a pattern in algal assemblage structure among regions according to nMDS with Flinders region separating from the other regions on the west coast (Naturaliste, Freycinet and Hamelin). Water temperature was the most influential of environmental variables, relative to exposure, substratum and depth (Figure 4). This was supported by a modest to strong Pearson correlation (Fowler & Cohen 1990) between algae and water temperature (R = 0.699) that was higher than Pearson R-values for other environmental variables (Table 3).

Table 3

Pearson correlations (R - values) between the biological and environmental variables examined.

	Mean depth	Exposure	Water temperature	Substratum
Algae	0.376	0.320	0.699	0.320
Fish	0.199	0.168	-0.011	0.168

On the west coast (Naturaliste, Freycinet and Hamelin regions), *Ecklonia radiata*, *Scytothalia dorycarpa* and *Platythalia quercifolia* dominated the macroalgae, whereas in the Flinders Bay region *Scytothalia dorycarpa*, *Kuetzingia canaliculata* and *Cystophora grevillei* were dominant. Some understorey species such as *Amphiroa anceps*, *Pterocladia lucida* and *Curdiea obesa* were found in all regions.

When comparing algal species distributions and richness among regions, Hamelin and Freycinet regions were combined (and referred to as Hamelin) due to their close proximity and the considerable overlap in algal assemblages found in each region (Figure 4). Species richness increased moving south, and twice as many algal species were recorded in the Flinders region compared to the Naturaliste region (Figure 6). Forty-four out of 205 species, representing around 21%, were common to all regions, while 41.5% were found in only one region which indicates a moderate degree of geographic distinctness. Around 25% of algae recorded from the Flinders region were 'endemic' to that region (in the context of this study), which was higher than either the Hamelin (11%) or Naturaliste (6%) (Figure 6).

Discussion

The interaction of the Leeuwin and Capes Currents creates unusual environmental conditions in the Capes region of Western Australia. As a likely effect of the warm southward flowing waters of the LC mixing with the CC, the flora and fauna inhabiting the region show overlap between two biogeographic zones; the Central West Province and the Southern Province. This has been

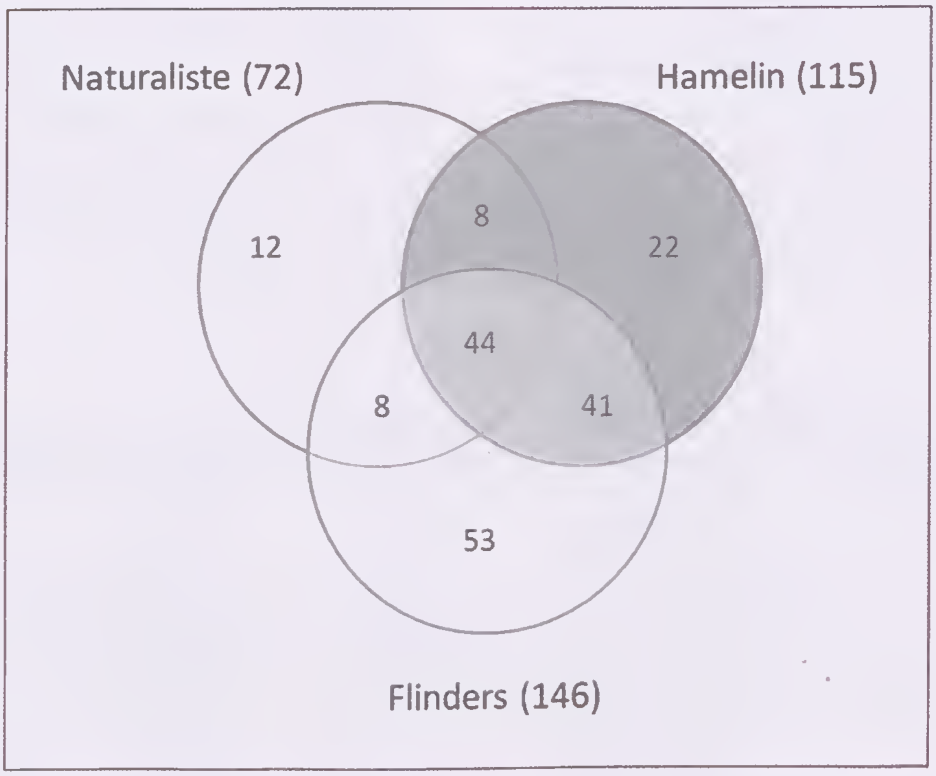

Figure 6. Venn diagram of the distribution of algal species among the regions. Note that Hamelin and Freycinet regions were combined into one grouping (Hamelin) in this analysis. Numbers in parentheses are the total number of species found within a region.

recognised in the Integrated Marine and Coastal Regionalisation of Australia with the designation of the Southwest Transition (Commonwealth of Australia, 2006) which encompasses the Capes region. This transition is reflected in the organisms inhabiting the Capes waters, with tropical and sub-tropical fish species identified in this and other studies, as well as range extensions of a number of algal species. A transition zone of 23° to 35°S was also suggested by Hutchins (1991) when describing the influence of the LC on fish species.

This study has used biological data from an existing project in the Capes region correlated with physical structuring variables to investigate the potential role of the LC, and in particular water temperature, on the fish and algal assemblages of the Capes region. Data have also been introduced from other studies on the effects of the LC on fishes and algae.

Scales of effect

In terms of broadscale distributions of species, the data indicate a number of fish species that are outside their generally accepted range. That is, species were encountered that would normally be expected in more tropical marine environments than the 33 to 34° S latitude of the Capes region. Forty six percent of fish species recorded were regarded as tropical, subtropical or sub-tropical – temperate. These results and the findings of other studies (Ayvazian & Hyndes 1995; Hutchins 1991), support the classification of the Capes region as part of the aforementioned transition zone between tropical and temperate waters.

The work of Hutchins (1991) indicates that the impact of the LC on shallow marine reef fishes in the Capes region is less than that at Rottnest Island, which may be expected given the more southward location of the Capes region and the cooler waters. Hutchins recorded 61 species of reef related tropical fishes at Rottnest Island and four in the Capes region.

The mean SST recorded in the Capes region from the NOAA data (NASA, 2007) was 19.26°C. This compares with the SST at Cape Mentelle (also in the Capes region) of 19.25°C (Pearce & Pattiaratchi 1999). Mean SST further north, where the LC also been linked to the structure of marine biotic assemblages, range from 26°C at Ningaloo (Westera 2003; Sleeman *et al.* 2007), 22°C at the Houtman Abrolhos Islands (Pearce 1997) and 21°C at Rottnest Island (Pearce & Faskel 2001). The decrease in water temperature with increasing latitude is consistent with the lower numbers of species of tropical or subtropical origins.

The small number of southward range extensions noted for algal species suggests that the LC does not strongly influence the distribution of algae in the regions studied. Phillips (2001) contends that the LC has definitely had an influence on extending the range of tropical species to the southern coasts of WA. However, the CC may obstruct southward dispersal along the coast (Wernberg *et al.* 2003) since it flows northwards and hence counters the LC. In this study, all algae recorded except for one species (*Rhodopeltis borealis*) have what could be considered a temperate distribution. While it is likely that tropical algae are carried southwards by the LC during years of strong flow, they probably establish as isolated populations (Phillips 2001) and as such may not be regularly encountered. The combined effects of the LC and the CC creates a very large transition zone between tropical and temperate floras (Wernberg *et al.* 2003).

Northward or westward range extensions were more common among the algae recorded in this study. While this may be partly attributed to algal spore dispersal by the northerly flowing CC, it is likely to also be largely due to the relatively few algal collections from the Capes region. The Flinders and Freycinet regions, in particular, have had little attention prior to this study in terms of the algal flora.

Variability was noted at a regional scale (within the Capes region) in terms of differences in algal (but not fish) assemblages. Regions on the west coast of the Capes that experience warmer waters were different to those in Flinders Bay further south. However the west coast sites are more exposed to wave and storm activity. Sites at the Hamelin region were of a similar depth to Flinders (10 m) but the Freycinet and Naturaliste regions were deeper (15–18 m) which may also have influenced the observed differences.

Smaller scales of effect on marine communities of the Capes are also likely, driven by depth, substratum type and exposure. These all showed weak Pearson correlations with the algal assemblages. Other factors not examined in this study that would likely influence the marine biota are topographic complexity, light to the benthos and sediment cover (Harman *et al.* 2003; Kendrick *et al.* 2004; Harvey 2005; Wernberg *et al.* 2005; Toohey 2007).

Larval transport

The distributions for some of the fish and algal species in this study may be influenced by changes in water temperatures resulting from the flow of the Leeuwin and Capes Currents, but may also be due to the physical transport of propagules from the warmer northern and cooler southern areas. Although algal propagules have been demonstrated to mostly settle within a short distance of the parent (Hoffmann 1987), currents have been shown to transport drift algae over long distances, particularly positively buoyant species such as *Sargassum* and their associated epiphytes (Womersley 1987; Walker 1991). Walker (1991) hypothesised that although the potential for the LC to transport algal propagules is reduced in comparison to faunal larvae, there is the potential for drift algal dispersal to extend the range of algal species. Goldberg *et al.* (2004) also reported limited dispersal of algal propagules with the species richness of algal canopy assemblages being maintained locally at the Recherche Archipelago, on the south coast of Australia.

The LC is, however, capable of transporting tropical fish eggs and larvae in a southwards direction and has the potential to extend the range limits of these species (Hutchins 1991). The effect of the LC on fish recruitment is strongly identifiable by comparing the south-east and south-west coasts of Australia. In south-east Australia, transport of fish propagules occurs in summer, whereas southerly transport in south-west Australia occurs in winter with the strongest flow of the LC. The timing of transport is more favourable to larval recruitment on the east coast as it coincides with the breeding period of most tropical fish (Hutchins 1991), whereas the southerly transport by the LC in the winter months, when water temperatures are falling and fish breeding is limited, is likely to create conditions where only the hardiest of fish larvae are likely to survive and recruit (Hutchins 1991).

Diversity

The number of fish species recorded in these surveys is comparable with other surveys of fishes in temperate Western Australia. In the Recherche Archipelago a study using DOV techniques recorded 90 species of fishes, many in common with the Capes surveys (Harvey 2005; Harvey *et al.* 2005). The Capes region does, however, distinguish itself through the high fish endemism characteristic of the south west coast. Fox & Beckley (2005) (p 403) stated that the south west coast was an endemism 'hotspot' when compared to other regions along the west Australian coastline.

The number of algal species recorded in this survey (205 species) was comparable with other studies on the temperate Western Australian coast (Table 4). The consistently high species richness from Jurien to the Recherche Archipelago may be due to the LC.

Water temperature within the Capes region may be one factor influencing marine assemblages within the region, but habitat is likely to be equally important. Relief and rugosity of substratum have not been evaluated here but are likely to provide further explanation of differences among regions. It is likely that the diversity of habitats in the region exerts a stronger role in shaping species assemblages on a regional scale (*i.e.*, within the Capes region) than the effects of the Leeuwin and Capes Currents.

This study was not originally intended to investigate the effects of the LC on marine biotic assemblages of the Capes region. However, the data indicate a broadscale effect of the LC on the Capes region in terms of the number of tropical, subtropical and particularly subtropical-temperate fish species recorded. This is consistent with other studies (Hutchins 1991; Lenanton *et al.* 1991; Ayvazian & Hyndes 1995) that showed an effect of the LC on the distribution of fish species. In the future, human induced climate change is also expected to lead more southerly distributions of marine biota on the West coast of Australia (Greenstein & Pandolfi 2008).

Table 4

Algal species richness at locations from the Western Australian coast for comparison with the Capes region.

Location	Species richness	Reference
Capes (Geographe Bay to Flinders Bay)	205	This project
Jurien	280	(Keesing & Hine 2005)
Geographe Bay (Quarries to Bunbury)	243	(Keesing & Hine 2005)
Perth metropolitan coast	229	(Keesing & Hine 2005)
Marmion Marine Park	202	(Simpson & Ottaway, 1987)
Marmion Marine Park	152	(Wernberg *et al.* 2003)
Recherché Archipelago	240	(Goldberg & Kendrick, 2005)

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Historical and contemporary influence of the Leeuwin Current on the marine biota of the southwestern Australian Continental Shelf and the Recherche Archipelago

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Abstract

The influence of the Leeuwin Current on the marine biota of the southern continental shelf of Western Australia is investigated by incorporating geological, oceanographic and evolutionary contexts. The effect of this seasonal current was found to have had an influence for approximately 40 million years as inferred from palaeontological evidence. The effect has been observed despite significant variation in the southward movement of the Leeuwin Current, sea level fluctuations, continental climate and the northward movement of the Australian continent. The marine flora and fauna of the Recherche Archipelago demonstrated the scale of the Leeuwin's reach with macroalgae, demersal fish, molluscs and other invertebrates having greater affinity with the southern temperate flora and fauna, with a small percentage of subtropical species transported eastward on the Leeuwin Current. A more detailed comparison of benthic macroalgal assemblages indicated significant differences between the Recherche, the southern temperate flora in South Australia at Isles of St Francis and the southwestern flora at Hamelin Bay, near Cape Leeuwin. These macroalgal assemblages were characterized by multiple species differences among the regions but also very high local species turnover (alpha diversity) among locations within each region. The relatively warm water and low seasonal variability in sea temperatures associated with the winter flow of the Leeuwin Current may have played a major role in the persistence of warm water species on the southern coast and the high species turnover we have observed over 18 degrees of longitude. The Leeuwin Current has played a major but not an exclusive role in the evolution and persistence of this flora as well as the species richness and endemism of other marine organisms along the southern coast of Western Australia.

Keywords: Leeuwin Current, Recherche Archipelago, southern Western Australia, evolution, macroalgae, diversity, alpha diversity

Introduction

This paper characterizes the effect of the Leeuwin Current on biota along the southern shores of Western Australia and more specifically the effect of the Current on the Recherche Archipelago. We summarize a body of literature that includes the effect of geological and contemporary processes on the biology, distribution and behavior of marine organisms found along the south coast and then more specifically for Recherche Archipelago. As a case study, the relationship that assemblages of marine macroalgae in the Recherche Archipelago have with the flora of southwest and southern Australia is then addressed. The paper then concludes with hypotheses about the potential causal mechanisms for the biogeographic relationships.

The Continental Shelf of southern Western Australia

The continental shelf off southwestern Australia extends from Israelite Bay at the western edge of the Great Australian Bight to Cape Leeuwin, covers an area of nearly 65,000 km^2 and is characterised by a 30–65 km-wide continental shelf that slopes gently to a depth of 100 m. It contrasts with the flat and gently sloping shelf of the main Great Australian Bight region east of the Recherche Archipelago (James *et al.* 1994). Further offshore, the seafloor drops away quickly after the shelf break at between 100 m and 140 m depth. In the east, the shelf is up to 65 km wide and punctuated by the granitic islands of the Recherche Archipelago (Conolly & von der Borch 1967). These islands are scattered across the entire width of the shelf and extend for more than 160 km along the coast. Sediments around the Recherche Archipelago are characterised by marine biogenic carbonates offshore and silica rich sediments onshore, that are eroded from the granites and gneisses of the archaean shield that covers a large proportion of southwestern Australia (Ryan *et al.* 2007). The shelf varies between 30 km and

65 km in width to the west of the archipelago, but most islands in the western portions of the shelf occur within 8 km of the mainland (Conolly & von der Borch 1967).

Numerous canyons incise the continental slope to the west of the Great Australian Bight. These include the Pasley and Esperance canyons offshore from the Recherche Archipelago, and the Albany Canyon Group (>30 canyons), which dissect the continental slope at regular intervals between Hood Point and Point D'Entrecasteaux (von der Borch 1968). Recent sonar surveys in the Albany Canyon Group have shown that some individual canyons are up to 2000 m deep and 90 km long, and extend uninterrupted between the shelf-break and the abyssal plain (Exon *et al.* 2005).

The southern continental shelf is heavily influenced by large, deeply abrading ocean swells that erode the shelf in depths up to 100m, with greatest abrasion of the bottom in the mid shelf region between 50 and 90 m depths (James *et al.* 1994). Contemporary sediments do not accumulate and the sediments that do accumulate are mixtures of reworked Pleistocene and recent sediments (Conolly & von der Borch 1967). An example of the scale of the effect of ocean swells on the south western continental shelf can be gleaned from Hemer (2006) who, in determining combined shear stress across the whole of the Australian continental shelf, found that in 48 metres depth off Cape Naturaliste, Western Australia, mean (maximum) wave periods recorded were 7.5 sec (15.7 sec), significant wave heights were 2.2 m (11.5 m) giving a combined benthic shear stress of 1.20 Nm^{-2} (85.9 Nm^{-2}), making it one of the highest energy sites in temperate Australia.

Palaeo-oceanography and the Leeuwin Current

The effect of the Leeuwin current or earlier proto – Leeuwin currents on water temperature and mixing of tropical species along the temperate south coast of Western Australia has been effective since the middle to late Eocene (35–42 Mya) (McGowran *et al.* 1997). Pelagic and benthic Foraminifera has been used to build a chronological palaeo-history of warm water transport southward along the west and south western coasts of Australia (Cann & Clarke 1993; Wells & Wells 1994; Mc Gowran *et al.* 1997; Li *et al.* 1999) There have been documented geological periods when the current seems to have been inactive (Early to Middle Oligocene, Early Pliocene) and reactivated (Early to Middle Miocene). The Leeuwin current strengthened in the middle to late Pleistocene and enhanced the southward transport of more tropical species (*Anadara trapezia* arcoid bivalve and *Acropora* corals) in southwest Australia and the inshore surface water temperatures during the last interglacial (122 –120 kyr BP) were > 2°C than they are today (Kendrick *et al.* 1991; McGowran *et al* 1997; Murray-Wallace *et al.* 2001). More recently during the late Quaternary, water north of 18°S varied little in temperature despite large extremes in climate, whereas further south there was significant changes to surface water temperatures, suggesting southward influence of the Leeuwin Current was disrupted during both glacial and interglacial extremes (Wells & Wells 1994).

There is a strong longitudinal temperature gradient and faunal pattern along the southern coastline of Western Australia generated by the Leeuwin Current. Larger benthic foraminifera show a west to east gradient in occurrence along the southern coast of Western Australia, with the genera *Heterostegina, Amphistegina, Amphisorus* and *Planorbulinella* common in sediments at Cape Leeuwin (115°S), *Amphistegina, Amphisorus* and *Planorbulinella* at Albany (117°S), and only *Amphisorus* at Esperance (122°E) (Li *et al.* 1999). At Esperance, the presence of tropical foraminifera, especially the benthic *Amphisorus* (*Marginopora*) taxon, both as living and in reworked sediments (120,000 yr BP) infer that the southward movement of the historical and contemporary Leeuwin Current has heavily influenced the benthic assemblages in this region at least since the last interglacial (Cann & Clarke 1993; Li *et al.* 1999).

As the Leeuwin Current seasonally flows during winter months and is episodic in strength of flow and influence on the south coast, it is quite amazing that it has such long geological time scale influences on benthic organisms as demonstrated for the arcoid bivalves (Kendrick *et al.* 1991) and benthic and pelagic foraminifera (Li *et al.* 1999).

The effects of sea level fluctuations and wave abrasion over the same geological period do not appear to weaken the overriding influence of the west to east gradient in the strength of the Leeuwin Current. Interestingly, Li *et al.* (1999) found the benthic foraminiferal assemblages during the late interglacial period were representative of lagoonal environments whereas recent assemblages were more representative of shallow open shelf environments.

The Contemporary Leeuwin Current on the South Coast of Western Australia

The Leeuwin Current moves eastward over the western shelf (Albany to Bremer Bay) moving offshore near the shelf break further eastward (Recherche Archipelago) and is strongest during winter. It warms sea-temperatures, and bathes the coastline with low nutrient waters. Light is generally less limiting to benthic and planktonic primary producers on the inner continental shelf and water column attenuation coefficients are very low, as water column turbidity from phytoplankton blooms and from river discharges are small (k_d = 0.08: Carruthers *et al.* 2007). The surface waters of the southwestern Australian shelf, waters of the Leeuwin Current and surface waters offshore are very low in nitrogen (less than 0.5 μmol) year round and primary productivity is nitrogen limited (Lourey *et al.* 2006).

Characteristics of Flora and Fauna on the south coast

The southwestern corner of Australia is a region of high species diversity and endemism for many marine organisms; for example, marine macroalgae (Womersley 1990; Phillips 2001), invertebrate taxa such as molluscs and echinoderms and decapod crustaceans(Wells *et al.* 2005; O'Hara & Poore 2000), and nearshore (Hutchins 1994) and continental slope demersal fish (Williams *et al.* 2001). High species richness in the region is attributed to the lack of mass extinction events associated with unfavorable environmental conditions – such as glaciation – over the recent geological past, and the moderating influence of the Leeuwin Current since the

Eocene (McGowran *et al*. 1997). The high endemism of the region is a product of long isolation of the marine flora and fauna as Australia has been separated from other land masses for the past 80 million years (Veevers 1991; Phillips 2001).

Effects of Leeuwin Current on Demersal and Migratory Fish

The Leeuwin Current is regarded as the dispersal mechanism responsible for transporting subtropical and tropic fish species southwards along the west coast (Hutchins & Pearce 1994) and eastwards along the south coast of Western Australia. The south coast of Western Australia is dominated by temperate demersal fishes that are found across the whole southern shores of Australia, although there are increasing numbers of sub tropical species from Israelite Bay to Cape Naturaliste (Hutchins 2001). Only 56% of demersal fish species are shared between the south coast, from Israelite Bay to Cape Naturaliste, and the lower west coast, Perth to Port Denison, and only 29 % with the central west coast, from Houtmans Abrolhos to Kalbarri. (Hutchins 2001). This influence is not as strong in surf zone fish assemblages. There is a decrease in total number of surf zone fish species from the west coast (20–66 species) to the south coast (11–16 species), and also a notable absence of tropical species in surf zone assemblages from the south coast (Ayvazian & Hyndes 1995).. The influence of the Leeuwin Current is also evident on recruitment and recruitment limitation. For example in pilchards (*Sardinops sagax*) along the south coast (Fletcher *et al*. 1994) there was a strong eastward transport of pilchard eggs from Albany over 150 km distances within days during winter when the Leeuwin Current was at its strongest but not during summer, resulting in geographical discontinuities in the early life histories of some populations of pilchards. This suggests that the Leeuwin Current influences fine spatial scale population structure in this highly mobile species. Interestingly, other highly mobile species are less influenced by the Leeuwin flow. The Australian herring (*Arripis georgiana*) is highly migratory and can be treated as a single stock from Victoria to southern Western Australia (Ayvazian *et al*. 2004).

Effect of the Leeuwin Current on Zooplankton

Both chaetognaths and siphonophores were better represented and more speciose during winter than summer (Gaughan & Fletcher 1997). Numbers of species decreased along 11 cross-shelf transects between Albany and Esperance in winter but not summer and this gradient reflected the decline in numbers of tropical species entrained in the Leeuwin Current during winter. The species of siphonophores and chaetognaths observed were all characteristic of warm waters and no cold temperate species were found.

Effect of the Leeuwin Current on Echinoderms and Decapod crustaceans

O'Hara & Poore (2000) analysed the distributions of 739 species of temperate Australian echinoderms and decapod crustaceans and noted that the western peak in species diversity at Perth, Western Australia, was 2 degrees further south than the eastern peak in species diversity at Sydney, New South Wales. Their interpretation of the geographical peaks in species richness should be taken with caution as it is confounded by sampling intensity and the proximity of Perth and Sydney to State and commonwealth Museum and research groups specializing in invertebrates. There were many endemic subtropical and tropical species characteristic of the lower west coast and their more southern distribution was due to the influence of the Leeuwin Current in transporting subtropical and tropical species southwards. The south coast of Western Australia from Albany to Eucla varies by only 2 degrees latitude and has a few degrees change between summer and winter water temperatures. O'Hara & Poore (2000) found relatively high species turnover, or replacement, across this region and inferred that the higher winter temperatures (Leeuwin Current) and small differences between summer and winter temperatures have allowed subtropical species to persist further east than may be expected. This results in a longitudinal turnover from more subtropical species to the west to more temperate species to the east but with little change in species richness.

Effect of the Leeuwin Current on Macroalgae

Wernberg *et al*. (2003) combined quantitative surveys of macroalgal diversity on limestone reefs from Marmion, north of Perth, Hamelin Bay and Hopetoun and concluded that there was a cline in overlapping species distributions from the west coast to the south coast. Wernberg *et al*. (2003) inferred that this cline indicated mixing of species from north to south, presumably through transport of propagules in the Leeuwin Current. They also found a shift in dominant canopy algae from the eurythermal *Ecklonia radiata* kelp forests common on the west coast to *E. radiata* combined with more southern temperate *Scytothalia doryocarpa* and *Cystophora* in the central south coast.

Influence of the contemporary Leeuwin Current on the Recherche Archipelago

The Recherche Archipelago is a group of 108 islands and many small reefs between 122°E and 124°E longitude. They are predominantly inshore on the shelf and are often not influenced by the main body of the Leeuwin Current that is situated on the outer continental shelf and slope at these longitudes. Interestingly, the Leeuwin current flows out to sea from the shelf break to the south of the eastern Recherche Archipelago, with an onshore movement of nutrient enriched sub-Antarctic waters (Cresswell & Griffin 2004). The effect of these colder nutrient-rich sub-Antarctic waters on the continental shelf near the Recherche Archipelago is unknown. Cresswell & Griffin (2004) postulate that this southward movement of the Leeuwin Current may be due to the 30° change in shelf orientation or the outflow of warmer waters from the Great Australian Bight or a combination of both. This offshore movement of the Leeuwin Current generates the strong anticyclonic eddies that develop south of the shelf break and are characteristic of waters south of the southern Western Australian continental shelf. The Recherche Archipelago is only seasonally bathed in Leeuwin Current waters and water temperatures are generally colder than offshore waters, and inshore waters to the west except for the months October and November (Figure 2 in Cresswell & Griffin 2004). Thus the overall strength of the Leeuwin Current may heavily affect the year to year influence on the biota of the Recherche Archipelago.

Floral and Faunal characteristics of the Recherche Archipelago

We first summarise the contemporary distribution of the predominant benthic biota, and demersal fish in the Recherche Archipelago. Then, using the macroalgae as an example, we investigate what makes this region interesting and how it is related to the temperate flora to the east and the subtropical and tropical flora associated with the west coast of Western Australia and the Leeuwin Current. We describe the importance of consistent ocean climate over millennia and its influence on the diversity and endemism of the macroalgal flora and incorporate both contemporary ecology and historical biogeography in the description of the effects of the Leeuwin Current on the marine benthos in this region.

Benthic Macroalgae of Recherche

Subtidal macroalgal assemblages of the Recherche Archipelago were more similar to macroalgal assemblages in South Australia and Victoria (Collings & Cheshire 1998; O'Hara 2001) than to those previouslydescribed from the west coast and the southwestern region of Western Australia (Wernberg *et al.* 2003). Two hundred and forty two species have been recorded in the Recherche Archipelago, with 148 species of Rhodophyta, 65 species of Phaeophyceae, and 29 species of Chlorophyta (Goldberg & Kendrick 2005) (Table 1). Range extensions were recorded for 37 species, 28 were westward extensions from the temperate southern coast of Australia and 9 were eastern extensions from southern and western shores of Western Australia west of the Archipelago (Goldberg & Kendrick 2005). This demonstrates the temperate nature of algal assemblages in the Recherche Archipelago and also our poor knowledge of the marine flora along southern Western Australia.

Marine Fauna of the Recherche Archipelago

Hutchins (2005) found the nearshore demersal fish fauna of the Recherche Archipelago totalled 263 species, with 68 species found only in Western Australia (Table 1). A barrier to eastward species dispersal was postulated to exist at the western side of the Great Australian Bight. Wells *et al.* (2005) identified 347 species of molluscs from the Recherche Archipelago, 275 were temperate southern Australian and 56 were Western Australian in distribution (Table 1). McDonald & Marsh (2005) describe 12 seastars from the Recherche Archipelago, all but one with a temperate southern distribution (Table 1). Similarly, of the 6 ascidians identified from Recherche, all had temperate southern distributions (McDonald 2005). Seventy seven hydroids were recently described from the Recherche Archipelago, 6 new species only known from the Archipelago, 58 with southern temperate distributions and only 5 restricted to Western Australia (Watson 2005). Pycnogonids have more west coast species (6) than southern temperate (5) and 1 new species only known from the Recherche Archipelago (Bamber 2005), although this trend has more to do with the geographical sampling done by the expert than the realised distributions of pycnogonids.

In summary, the marine flora and fauna of the Recherche Archipelago are predominantly temperate southern Australian in affinity. There are few species that have west coast distributions, supporting the model that the Recherche Archipelago is less influenced by the Leeuwin Current. Interestingly, the Leeuwin Current may still act as a barrier to western transport of southern Australian temperate species. This requires further investigation.

Relationship of the macroalgal flora of Recherche Archipelago with Hamelin Bay, WA and the Isles of St Francis, South Australia

Our objective was to test if the marine flora of the Recherche Archipelago (RA) was similar to that of representative floras of the south west flora documented at Hamelin Bay, Western Australia or the southern Australian flora east of the Great Australian Bight, from the Isles of St Francis, near Ceduna, South Australia. Rather than a full biogeographical analysis like that of O'Hara & Poore (2000), we have focused in on specific localities that are representative of the south western region (Wernberg *et al.* 2003; Kendrick *et al.* 2004; Toohey *et al.* 2007) and the southern region, east of the Great Australian Bight (Womersley & Baldock 2003). This decision was made because floristic sampling along the southern shores of Western Australia have been limited to a few field surveys and the taxonomic data from

Table 1

Description of the species richness and relationships of selected groups of the flora and fauna of the Recherche Archipelago with western and southern temperate Australia.

Taxon	Recherche Species Richness	Only known from Recherche	Southern Temperate Australia	Western Australia	Author
Seaweeds	234	0	186	17	Goldberg & Kendrick 2005
Fish	263	0	189	68	Hutchins 2005
Molluscs	347	0	275	56	Wells *et al.* 2005
Sea stars	12	0	11	1	McDonald & Marsh 2005
Ascidians	6	0	6	0	McDonald 2005
Hydroids	77	6	58	5	Watson 2005
Pycnogonids	15	1	5	6	Bamber 2005

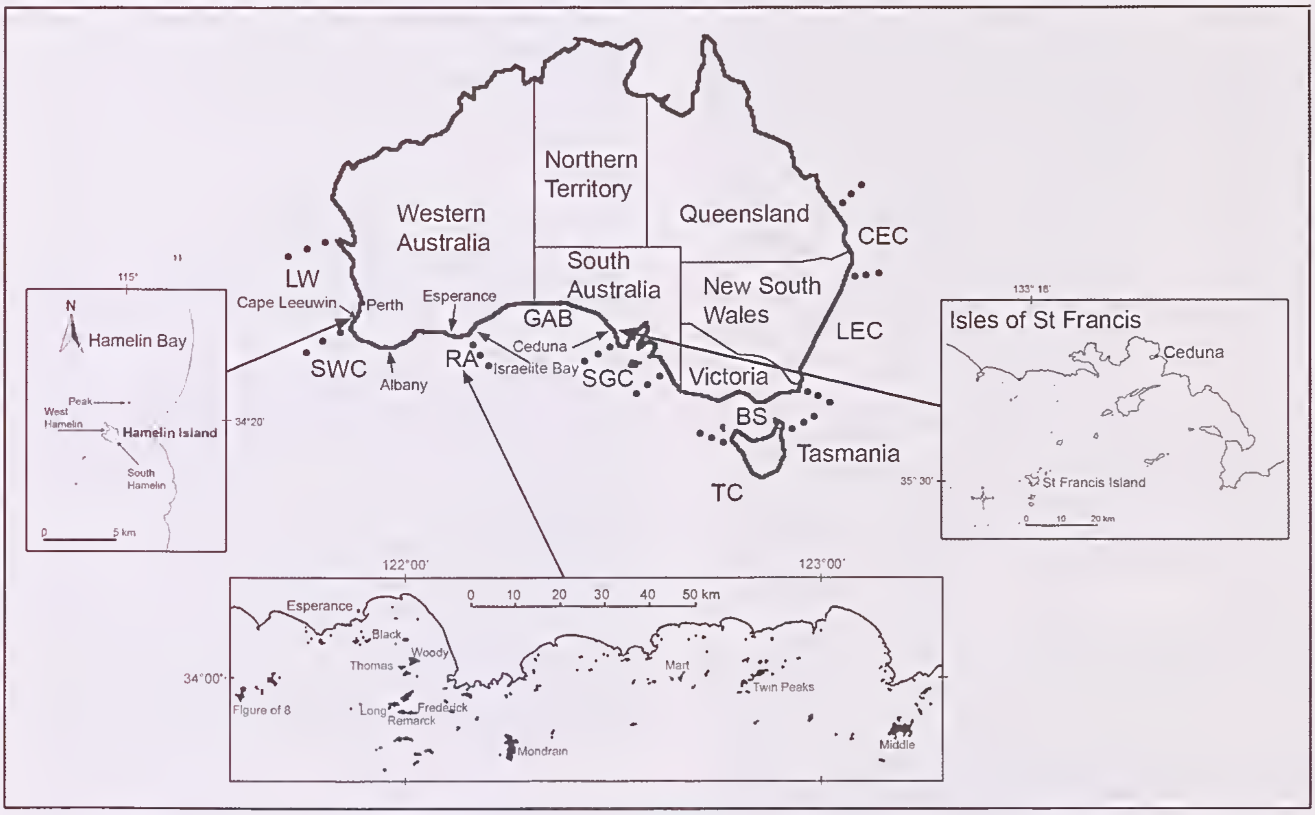

Figure 1. A. Map of Australia showing locations mentioned in the text and the CONCOM marine biogeographic regions LWC = Lower West Coast, SWC = South West Coast, GAB = Great Australian Bight, SGC = South Gulfs Coast, BS = Bass Strait, TC = Tasmanian Coast, LEC = Lower East Coast, and CEC = Central East Coast and the Recherche Archipelago (RA), with inset maps of the three study locations: Hamelin Bay, Recherche Archipelago and Isles of St Francis.

opportunistic collections, many from the drift on beaches (see Womersley 1984, 1987, 1994, 1996, 1998, 2003)

Species presence information for macroalgae for the south west flora were taken from collections made in 2006 from 18 locations in Hamelin Bay (n = 54 x 0.25 m^2 quadrats) (Figure 1) . This is part of a 6 year temporal study described in Kendrick *et al.* (2004) and Toohey *et al.* (2007). The Recherche Archipelago flora was compiled from surveys of 11 islands (Figure 1) conducted in October of 2003 and 2004 (n = 372 x 0.25 m^2 quadrats) (Goldberg & Kendrick 2004; Goldberg *et al.* 2006). Similar species data was taken from a survey of the Isles of St Francis from 12 locations (Figure 1) by Womersley & Baldock (2003). These data differ from the other locations as they are not quadrat samples but actual species lists from each location.

Multivariate tools were used to illustrate differences among floras in the southern coast of Australia. Non-metric multidimensional scaling (MDS) was used on a Bray-Curtis similarity matrix of species presence/absence data, equivalent to a Sorenson coefficient, from all three regions (PRIMER Vers. 6). A one-way permanova tested the significance of differences in macroalgal assemblages among Isles of St Francis, Recherche and Hamelin Bay (Anderson 2001). A similarity percentages analysis was conducted to assess the average similarity within versus among regions.

We found all three regions separated clearly in two dimensions on the MDS plot (Figure 2). They did not form a cline as demonstrated by Wernberg *et al.* (2003) for the south western algal flora, but were distinct groupings. Both Hamelin Bay (SW) and the Recherche Archipelago (RECH) formed tight clusters whereas the locations from the Isles of St Francis (FRANCIS) were more dispersed. This difference was possibly driven by the difference in sampling intensity between regions; Isles of St Francis were qualitative species lists made from collections at locations whereas both Recherche and Hamelin Bay were quantitative samples taken using quadrats. The permanova on species presence/absence (Table 2) and pairwise tests between regions (Table 3) demonstrated that macroalgal assemblages in all 3 regions were highly significantly different.

The average similarity accounted for by among and within regions demonstrates some overlap in species presence/absence among regions (Table 4). The macroalgal assemblage in Hamelin Bay (SW) shared almost 25% with the Recherche Archipelago (RECH) but only 14% with the Isles of St Francis (FRANCIS). The Recherche Archipelago shared approximately 21% with the Isles of St Francis. Clearly, these flora are not that similar among regions. What is driving this difference? The shared similarity among locations with regions also is small (diagonals in Table 4). Locations within regions shared less than 50% of species for both Hamelin Bay and the Recherche Archipelago. From the species lists from the Isles of St Francis it was less than 22%. Clearly the macroalgal flora within each region shows high levels

Table 2

One- Factor Permanova comparing species presence macroalgal assemblage data from the 3 regions (Hamelin Bay, Recherche Archipelago and the Isles of St Francis) along the south western and central coast of Australia.

Source	df	MS	Pseudo-F	P(perm)
Regions	2	16243	8.8009	0.0001
Residual	41	1845.6		
Total	43			

Table 3

Pairwise comparisons between Hamelin Bay (SW), the Recherche Archipelago (RECH) and the Isles of St Francis (FRANCIS).

Groups	t	P(perm)	perms
SW, RECH	3.3896	0.0001	9872
SW, FRANCIS	2.2909	0.0001	7661
RECH, FRANCIS	3.0584	0.0001	9912

Table 4

A matrix of the average similarity of macroalgal assemblages within and among regions along the south western and central coast of Australia. SW = Hamelin Bay, RECH = Recherche Archipelago, FRANCIS = Isles of St Francis)

	SW	RECH	FRANCIS
SW	*48.71*		
RECH	24.96	*48.43*	
FRANCIS	14.40	20.61	*21.88*

of species turnover among locations. The species responsible for the differences among and within regions were many with no species contributing more than 1.6 % to the overall percentage of dissimilarity among the regions.

Discussion

The macroalgal flora and fauna of the Recherche Archipelago is more similar to the temperate flora found along southern shores of Australia. Separation of the south coast of Australia from Antarctica began approximately 90 million years ago and ended 30 million years ago with oceanic water flowing between the two continents (Poore 1994). During this period of separation between Australia and Antarctica, the macroalgal flora in the shared waters between the two continents was presumably Tethyan in origin (Phillips 2001). Clayton (1994) speculated that prior to formation of sheet-ice, Antarctic macroalgal species richness was similar to that of temperate southern Australia, particularly for species in the Phaeophycean order Fucales (*e.g.*, *Cystophora* and *Sargassum* species). Coastal sea temperatures have remained temperate as the continent moved with the northerly drift of the Australian plate, with a warm-water influx from the Leeuwin Current along the west coast (Phillips 2001). This has resulted in southward and eastward transport of subtropical species from central and northern Western Australia. These subtropical species are a small percentage of the predominantly temperate flora and fauna found in the Recherche Archipelago.

Species replacement (turnover) of the marine macroalgae from east to west along the southern shores of southwestern Australia is great, although, species

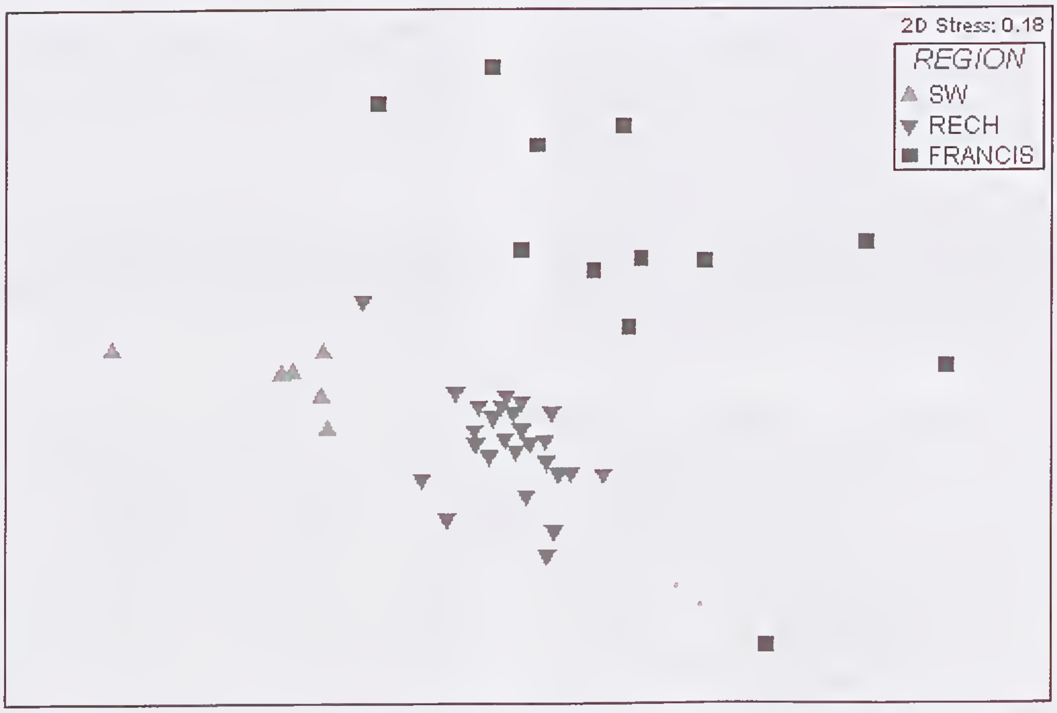

Figure 2. Non-metric two-dimensional multidimensional scaling plot (MDS) depicting the relatedness of subtidal macroalgal assemblages (using species presence) among SW (Hamelin Bay), RECH (Recherche Archipelago) and FRANCIS (Isles of St Francis).

richness from Isles of St Francis to Hamelin Bay is similar. The majority of the replacement is a switch from southern temperate species to endemic south western species to more prevalence of subtropical species suggesting an increase in influence of the Leeuwin Current from east to west. For example, subtropical and tropical species from central and northern Western Australia are a small percentage of the flora of the Recherche Archipelago. Echinoderms and decapod crustaceans show a similar east to west species replacement with little change in species richness (O'Hara & Poore 2000).

How can we account for the pattern in species replacement at local and regional scales across southern Western Australia? The contemporary Leeuwin Current aids in dispersal of tropical and subtropical species to the southern coast of Western Australia, depresses upwelling resulting in high ambient light conditions at depth and reduces the seasonal variation in nearshore seawater temperatures. Yet diversity of marine organisms as demonstrated by benthic algae in this study, and echinoderms and decapod crustaceans by O'Hara & Poore (2000) is not solely driven by contemporary processes alone. Historically the influence of warmer waters further south in temperate Australia has resulted in high diversity, endemism and local species replacement.

The long term effect of the northward drifting Australian continent and the moderating effect of the warm Leeuwin Current have resulted in a diverse and highly endemic marine macroalgal flora (Phillips 2001). Isolation can explain the endemism but what historically has produced and maintained the diversity? High local species replacement is a signature of the benthic macroalgae of this region (Kendrick *et al.* 1999, 2004; Goldberg & Kendrick 2004; Toohey *et al.* 2007). Wernberg *et al.* (2003) found 33% of nested variation in species richness was accounted for by local species turnover. Similarly, Goldberg & Kendrick (2004) found approximately 60% of all macroalgal species found in a detailed survey of 6 islands in the western Recherche Archipelago were rare, occurring as less than 5 gm wet weight across 216 quadrats where the average algal biomass from the quadrats was 1kg or more. Sixty percent of 220 macroalgal species accounted for this local scale species replacement. Kendrick *et al.* (1999) reported that similar high local species replacement, or turnover, was not accounted for by differences between reefs and exposure to ocean swells at Marmion, on the west coast of Western Australia.

What drives local species replacement? This is not associated with any broad scale oceanographic gradients but to the successful colonisation and maintenance of small local populations. What aspect of this marine environment is so unique that it has historically promoted and in contemporary time scales maintained such high alpha, or local diversity? Ecological theory about species coexistence suggests a series of interrelated processes support the high species turnover we have observed. Firstly, competitive networks can be decoupled and the major factor usually invoked is the frequency and extent of biological and physical disturbances. Competitive networks may also not be established if the assemblages are not density-dependent.

Macroalgal species can produce up to millions of reproductive propagules per thallus (Kendrick & Walker 2005), although dispersal is thought to be limiting as propagules have a small planktonic lifespan. Successful dispersal and recruitment into a density-independent adult population can result in decoupling of competition and the co-existence of many species. The stochastic nature of disturbance and recruitment temporally and spatially can also result in patchy spatial distribution of species, especially when associated with highly competitive species like the kelp *Ecklonia radiata*, common on temperate coasts of Western Australia. The frequency and size of the gap creating disturbance and time of recolonization of gaps in kelp forests determines the biomass and species richness of macroalgae in the assemblage (Toohey *et al.* 2007). Once competition from the kelp is reduced the number of species colonising the reef increases dramatically although the biomass of the assemblage is small. As the kelp recolonises the gaps species richness declines and overall biomass increases (Toohey *et al.* 2007).

The realized niche concept is poorly identified for marine benthic flora and fauna although much of the observed small scale species replacement may be driven by very fine scale differences in the reef that affect what species colonise it (Toohey & Kendrick 2008). Recent work on the effect of reef topography on assemblage structure and diversity of macroalgae has demonstrated that competitive interactions on complex reefs can be reduced and diversity increased through increasing niches and through niche overlap for foliose algae. Rugose, topographically complex reefs affect the strength and direction of competition by *Ecklonia radiata* (Toohey & Kendrick 2008). This spatial complexity enhances the number of species associated with kelp forests, whereas in a topographically poor planar reef the negative effect of kelps on the colonisation and persistence of other macroalgae is more evident (Kendrick *et al.* 1999; Toohey *et al.* 2007).

Other canopy forming macroalgae do not show similar competitive dominance. Goldberg (2007) demonstrated that patterns in algal colonisation under canopies of *Cystophora* and *Sargassum* in the Recherche Archipelago were maintained by processes other than competition with the canopy species. Clearly the effect of canopy can be uncoupled either by the release from competition via disturbance, provision of niches through reef rugosity or through mechanisms other than direct competition by canopy species.

Historically, the species rich benthic flora and fauna have persisted on the southern coast of Western Australia because it evolved in geographical isolation, has not suffered major extinction events, glaciation in recent geological past (Holocene) nor major shifts in currents since the Eocene (McGowran *et al.* 1997). Valdovinos *et al.* (2003) demonstrated that regional context and history defines the distribution and abundance of southern temperate Pacific molluscs. Their explanation for higher mollusc biodiversity in cold temperate waters than subtropical and tropical waters was the combined effects of increased continental shelf surface area, refugia during glaciation events and the divergence of species through geographical isolation associated with historical and present currents. Similarly, the lagoonal environments reported from benthic foraminifera assemblages during the late interglacial period (Li *et al.* 1999) suggest that benign environments for marine organisms have existed at least into the recent geological past. We report algal species replacement but no real change in species richness from east to west along the south-western Australian continental shelf. Hamelin Bay in the southwestern tip of Western Australia has an assemblage of algae distinct from that of the Recherche Archipelago, and the Isles of St Francis at the eastern extent of the Great Australian Bight. This rate of species replacement, or turnover, over 18 degrees of longitude in southern Australia has already been reported for decapod crustaceans (O'Hara & Poore 2002). Their explanation hinges on both global isolation and regional connectance of species across the whole southern temperate continental shelf over the last 80 million years, combined with warming of waters as Australia has moved northward resulting in isolation and extinction of some species and southward moving warm water currents from the tropics on both the western and eastern coasts of Australia bringing warm temperate, subtropical and tropical species into more temperate latitudes. Local species replacement (alpha diversity) is extremely high in seaweed assemblages and we list what we believe are important local processes that have led to this situation. Similarly, Huston (1999) defines local processes (and their interaction with regional processes) in the evolution of diverse groups of organisms. He emphasizes the need for greater understanding of species niche concept and scaling studies of patterns in distribution and abundance such that they are sampled across scales that are relevant to the processes that have defined the survival and evolution of organisms. In benthic algae, local species turnover appears to be associated with release from competitive hierarchies, physical disturbance, high levels of recruitment and broad niche requirements.

In temperate Western Australia, historical and contemporary processes have resulted in a globally important, speciose endemic hotspot for marine flora and fauna. The Leeuwin Current has played a major but not an exclusive role in the evolution and persistence of this flora and fauna along the southern coast of Western Australia.

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The mean state of the Leeuwin Current system between North West Cape and Cape Leeuwin

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Abstract

The circulation and water mass characteristics offshore Western Australia between North West Cape and Cape Leeuwin (21–35° S) are described using findings from past studies as well as additional field data. The circulation pattern in the study region is dominated by the Leeuwin current system, which includes three main currents: the Leeuwin current (LC), the Leeuwin undercurrent (LU), and shelf current systems consisting of the Capes and Ningaloo currents. Localised discharges of fresh water and high salinity water were present in the shelf regions offshore Perth and Shark Bay, respectively. Localised upwelling also affected the water masses in the Geelvink Channel. Eight water masses were identified as interleaving layers of salinity and dissolved oxygen concentrations: (i) low salinity tropical surface water (TSW); (ii) high salinity south Indian central water (SICW); (iii) high dissolved oxygen subantarctic mode water (SAMW); (iv) low salinity Antarctic intermediate water (AAIW); (v) low oxygen north-west Indian intermediate (NWII) water; (vi) low oxygen upper circumpolar deep water (UCDW); (vii) high salinity low circumpolar deep water (LCDW); and (viii) cold (< 2 °C), high oxygen Antarctic bottom water (AABW). The LC consisted of tropical surface water and south Indian central water. In the northern region of the study area (between North West Cape and the Abrolhos Islands), SICW was present as a subsurface salinity maximum beneath the TSW. Between 28 and 29.5° S, the depth of the 35.7 salinity contour decreased from ~150 m to the surface. South of 29.5° S, SICW was present at the surface. Along the continental slope, the LU was present beneath the LC at depths between 300 and 800 m, with its core (lowest oxygen level) at 450 m. The LU transported SAMW north while the wind drove the continental shelf currents. Southerly, upwelling-favourable winds pushed the LC farther offshore (a process known as Ekman transport), which forced cold, upwelling water onto the continental shelf. The Ningaloo current mainly consisted of TSW and extended north from Shark Bay to beyond North West Cape; the Capes current consisted of SICW and was present as a continuous current system on the continental shelf, extending north from Cape Leeuwin to Geraldton—a distance of some 750 km.

Keywords: Leeuwin Current, Leeuwin Undercurrent, Ningaloo Current, Capes Current, water masses, Western Australia.

Introduction

Globally, eastern ocean basins are highly productive ecosystems, which support high primary productivity and large pelagic finfish stocks. The exception to this rule, however, is off the west Australian coast, where, although the wind regime resembles that of other eastern ocean margins, the waters are oligotrophic. Thus the first studies of the physical oceanographic processes off the west Australian coast contrasted the circulation off Western Australia with that from other eastern ocean margins, which led to the discovery of the Leeuwin current. Later studies addressed the Leeuwin current system dynamics and revealed the Leeuwin current system consisted of three main currents: the Leeuwin current, the Leeuwin undercurrent, and shelf current systems consisting of the Ningaloo and Capes currents.

The main contributors to the knowledge of the physical oceanographic processes off the west Australian coast have been Andrews (1977, 1983), Cresswell and Golding (1980), Hamilton (1986), Smith *et al.* (1991), Pearce and Walker (1991), Cresswell and Peterson (1993), Gersbach *et al.* (1999), Pearce and Pattiaratchi (1999), Fang and Morrow (2003), Feng *et al.* (2003, 2005), Morrow *et al.* (2003), Ridgway and Condie (2004), Fieux *et al.* (2005), Woo *et al.* (2006a, 2006b), Rennie *et al.* (2007), Meuleners *et al.* (2007), Woo and Pattiaratchi (2008), Batteen and Miller (2008).

The main surface and subsurface current systems (Figure 1) along the west Australian coast are:

- the West Australian current
- the Leeuwin current
- the Leeuwin undercurrent
- continental shelf current systems consisting of the Capes and Ningaloo currents
- Shark Bay outflow
- localised flow associated with topographic features, such as the Houtman Abrolhos Islands and the Perth Canyon.

Here we describe each of the above current systems and discuss the surface and subsurface water masses

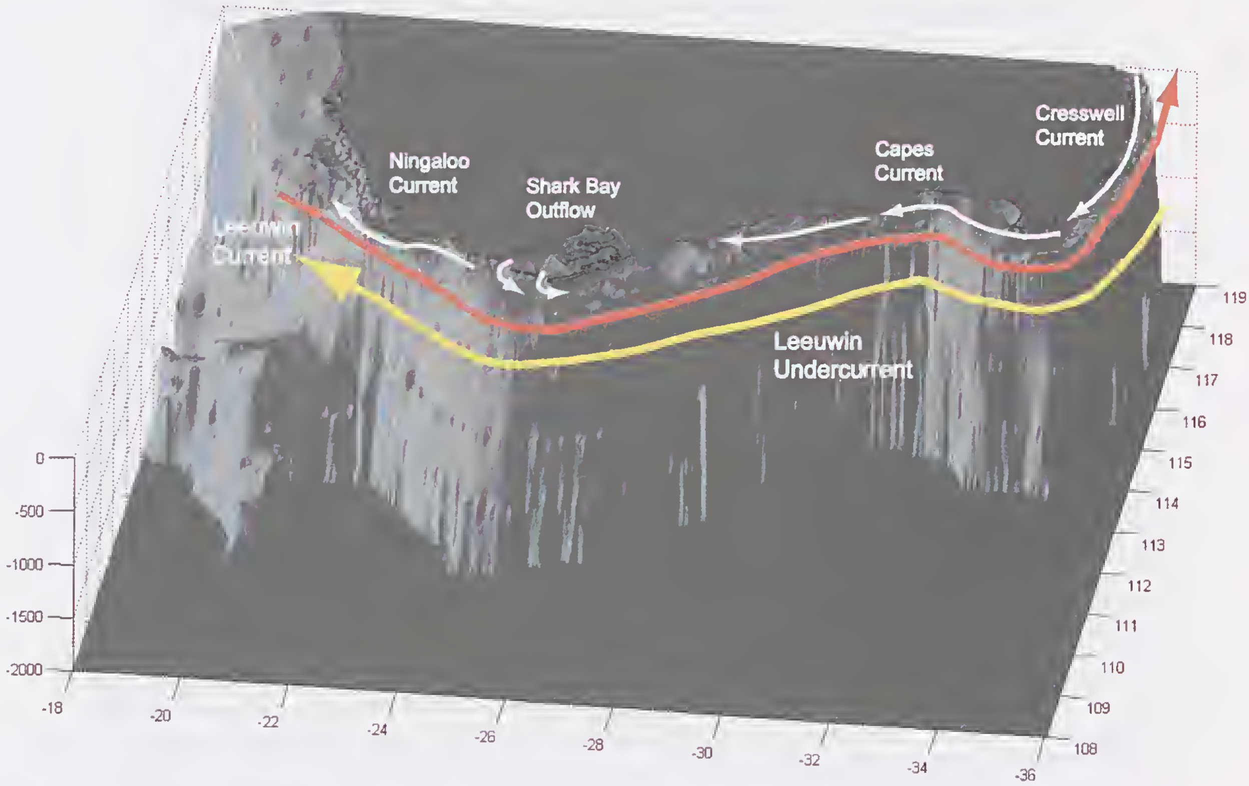

Figure 1. Schematic of the main surface and subsurface currents along the west Australian coast.

found in the study region. We also present data obtained from research voyages to the northern region (between North West Cape and the Abrolhos Islands) in November 2000 (ORV *Franklin* voyage no. 10/2000) and the southern region (between the Abrolhos Islands and Cape Leeuwin) in October/November 2003 (RV *Southern Surveyor* voyage no. 09/2003). Figure 2 shows the oceanographic station locations for both voyages.

Surface and subsurface currents

The West Australian current

Along most eastern ocean boundaries, equatorward eastern boundary currents are slower and wider than poleward western boundary currents and form one part of the anticyclonic subtropical gyre in each hemisphere's oceans. Sverdrup flow (the balance between wind stress, pressure gradients, and Coriolis acceleration) causes these gyres. Cool, upwelled water and high primary productivity, which supports the pelagic finfish industry, characterise eastern boundary current regions. The region offshore Western Australia does not have the same level of biological productivity as that induced by the Humboldt current off Peru or the Benguela current off Africa because the Leeuwin current (LC) suppresses the upwelling of cool, nutrient-rich water along the continental shelf (Pearce 1991).

The West Australian current is a shallow, equatorward surface current located farther offshore from the LC. It forms the eastern arm of the subtropical Indian Ocean gyre and its movement resembles the large, anticlockwise motion seen in southern ocean basins (Tomczak & Godfrey 1994). Schott and McCreary (2001) proposed that the equatorward current was located a distance of more than 1000 km from the WA coast, and the width of it extended to 60°E.

Andrews (1977) suggested the West Australian current provided an eastward inflow of water to the LC at around 30–34° S and turned south near the coast between 29 and 31° S. Church *et al.* (1989) proposed the West Australian current turned south between 30 and 33° S and was entrained into the poleward LC flow. Cresswell and Peterson (1993) and Akhir and Pattiaratchi (2006) suggested the inflow from the West Australian current strengthened the LC as the LC rounded Cape Leeuwin and turned into the Great Australian Bight.

The Leeuwin current

The circulation off the west Australian coast is different from that off other western continental margins (Schott 1935; Smith *et al.* 1991). In each of the main ocean basins, the surface circulation forms a gyre with a poleward flow along the western margin of the basin and a gyre with an equatorward flow along the eastern margin. The eastern margins (off south America and south Africa, for example) are also areas of high productivity due to upwelling, except off the west Australian coast where the LC transports water poleward (Figures 1 and 3).

The LC is a shallow (< 300-m-deep), narrow (< 100-km-wide) band of warm, low salinity, nutrient-depleted water of tropical origin, which flows poleward from Exmouth to Cape Leeuwin and into the Great Australian Bight (Church *et al.* 1989; Smith *et al.* 1991; Ridgway & Condie 2004). The LC signature extends from North West

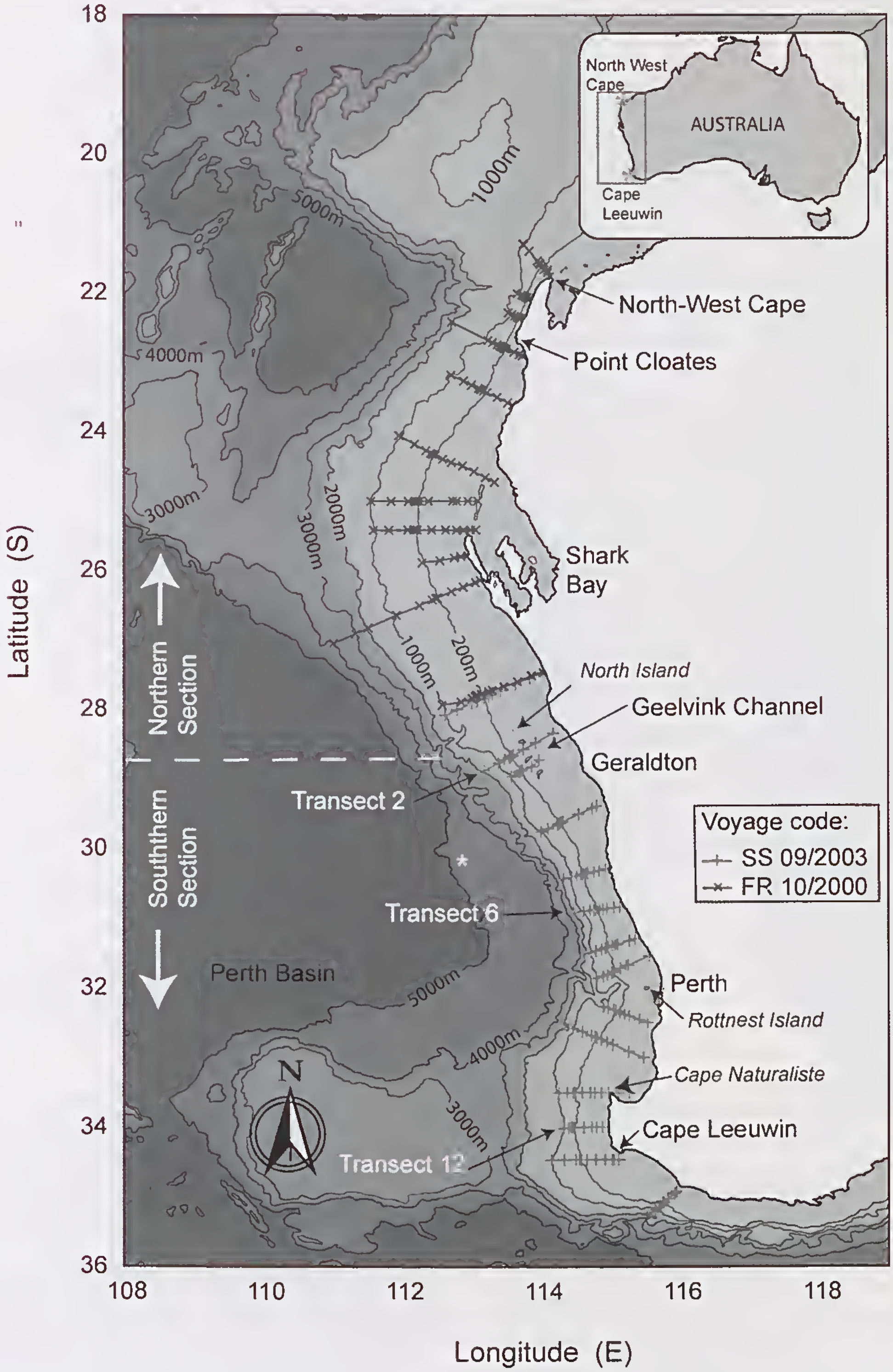

Figure 2. Bathymetry of the study region as well as the locations of the CTD transect lines and stations (from voyages SS09/2003 and FR10/2000), the meteorological stations (italics), and the deep water CTD station (*).

Cape to Tasmania as the longest boundary current in the world (Ridgway & Condie 2004). Cresswell and Peterson (1993), who defined the LC as a warm current of tropical origin, found that water from the West Australian Current increased the LC salinity in summer.

Warm, low salinity water from the Pacific Ocean, which flows through the Indonesian archipelago to the Indian Ocean, creates low density water (compared with the cooler, saltier ocean waters off south-west Australia) in the region between Australia and Indonesia. The resulting density difference, which sets up a sea level gradient of about 0.5 m along the west Australian coast, is the LC's driving force. The earth's rotation causes water from the Indian Ocean to be entrained into the LC as the LC flows south; thus the LC strengthens as it flows south.

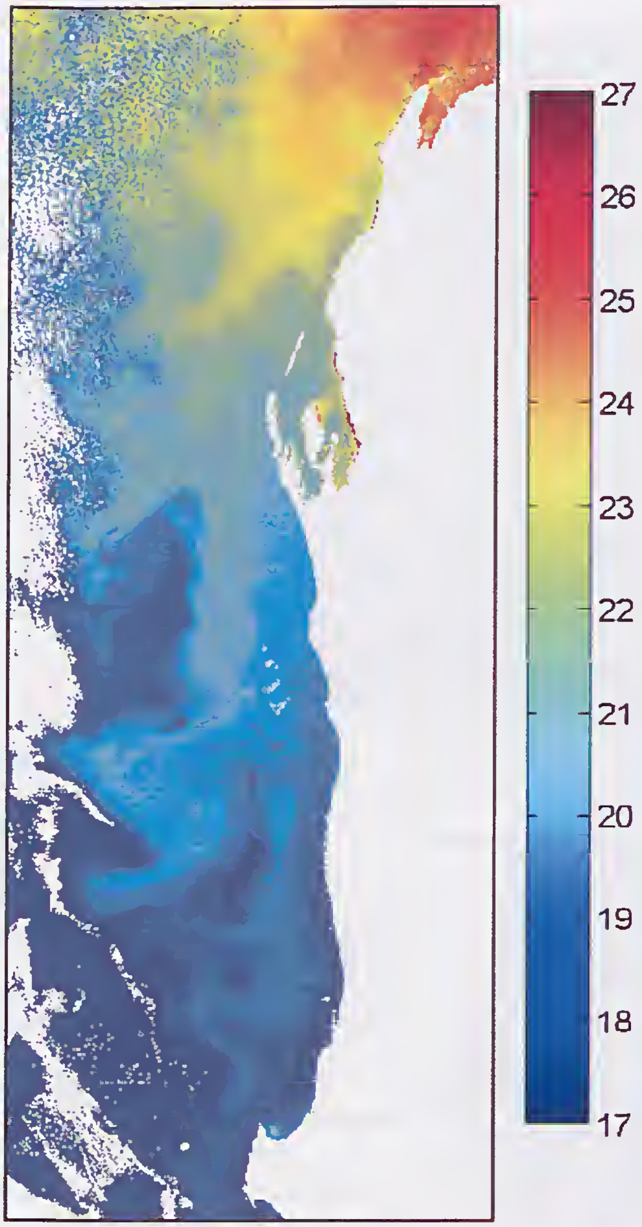

Figure 3. MODIS-derived satellite sea surface temperature image of the Leeuwin current obtained on 10 November 2007.

Studies have shown that along the west Australian coast, an alongshore pressure gradient, which overwhelms the opposing equatorward wind stress, drives the LC (Thompson 1984, 1987; Godfrey & Ridgway 1985; Weaver & Middleton 1989; Batteen & Rutherford 1990; Pattiaratchi & Buchan 1991). These studies found the alongshore pressure gradient of the sea surface slope was –4 x 10^{-7} (relative to the 300 dB). This pressure gradient overcomes the upwelling-favourable winds and induces an onshore surface flow, which causes downwelling at the coast. Woo & Pattiaratchi (2008) found that the alongshore geopotential gradient of the sea surface slope along the 1000-m isobath was –4 x 10^{-7} (from north to south) relative to the 300 dB level. Onshore geostrophic flow from the central Indian Ocean towards Western Australia occurs between about 15 and 35° S. Geostrophic inflow in the north (15–28° S) and tropical water from the North-west Shelf forms the LC's warm, low salinity core (Smith *et al.* 1991; Woo *et al.* 2006b; Woo & Pattiaratchi 2008). Meuleners *et al.*'s (2007) numerical modelling results confirmed that the mean annual transport across the LC at 30° S was 5.7 Sv (x 10^6 m^3s^{-1}), of which the northern boundary (at 26° S) contributed 3.60 Sv, or 63%. They estimated the inflow of water through the western boundary due to geostrophic balance at 2.1 Sv, or 37%, and found it varied meridionally.

The LC has a seasonal and inter-annual variability: it is usually stronger in winter and under La Niña conditions and weaker in summer and under El Niño conditions (Feng *et al.*, 2003). The LC transport is strongest near the shelf edge in late summer and early autumn, farther seaward in winter, when it carries around 5 Sv, and weakest in summer (~2 Sv). Its seasonal variability reflects changes in the local wind stress: the LC is weakest along the west Australian coast in summer as it accelerates into the maximum equatorward wind stress and strongest in winter because of the weak equatorward wind stress and the strong pressure gradient (Godfrey & Ridgway 1985). The LC is also weak in summer along the south Australian coast because the prevailing winds are from the east and south-east.

The Leeuwin undercurrent

Few studies have examined the Leeuwin undercurrent (LU); however, Thompson (1984, 1987), while studying the LC off the west Australian coast, observed the LU flowing beneath the LC (Figure 1). Thompson (1984) also found the LU transported 5 Sv of salty (> 35.8), oxygen-rich, nutrient-depleted water northward at 0.32–0.40 ms^{-1}. Current meter data from the Leeuwin Current Interdisciplinary Experiment (Smith *et al.* 1991) confirmed Thompson's (1987) findings and revealed the undercurrent was narrow and located adjacent to the continental slope between the 250 and 450-m depth contours.

Meuleners *et al.* (2007) used numerical modelling tests to show the LU had a maximum speed of 0.35 ms^{-1} (with a mean speed of 0.1 ms^{-1}) and consisted of meanders and eddies, which the more energetic LC induced. They found the LU core was located beneath the LC core at depths between 250 and 600 m, with the continental slope forming its eastern border. Meuleners *et al.* (2007) also found that the LU's northward transport increased as the water warmed and became saltier, which suggested that as the LU moved north, it entrained water from farther offshore in a similar way to the LC.

An equatorward geopotential gradient located at the depth of the undercurrent drives the LU (Thompson 1984). Geopotential anomaly values taken from 500 dB/3000 dB (Wyrtki 1971) and 450 dB/1300 dB (Godfrey & Ridgway 1985) revealed the LU's presence; Thompson (1984) and Smith *et al.* (1991) also recorded subsurface slopes of 0.4 x 10^{-7} and 0.2 x 10^{-7}, respectively. Woo and Pattiaratchi (2008) used field data obtained from a section along the 1000 m contour, parallel to the west Australian coast, to estimate a slope of 1 x 10^{-7}, which was the LU's equatorward driving force enhanced by an east-west subsurface slope generated by the downwelling of the

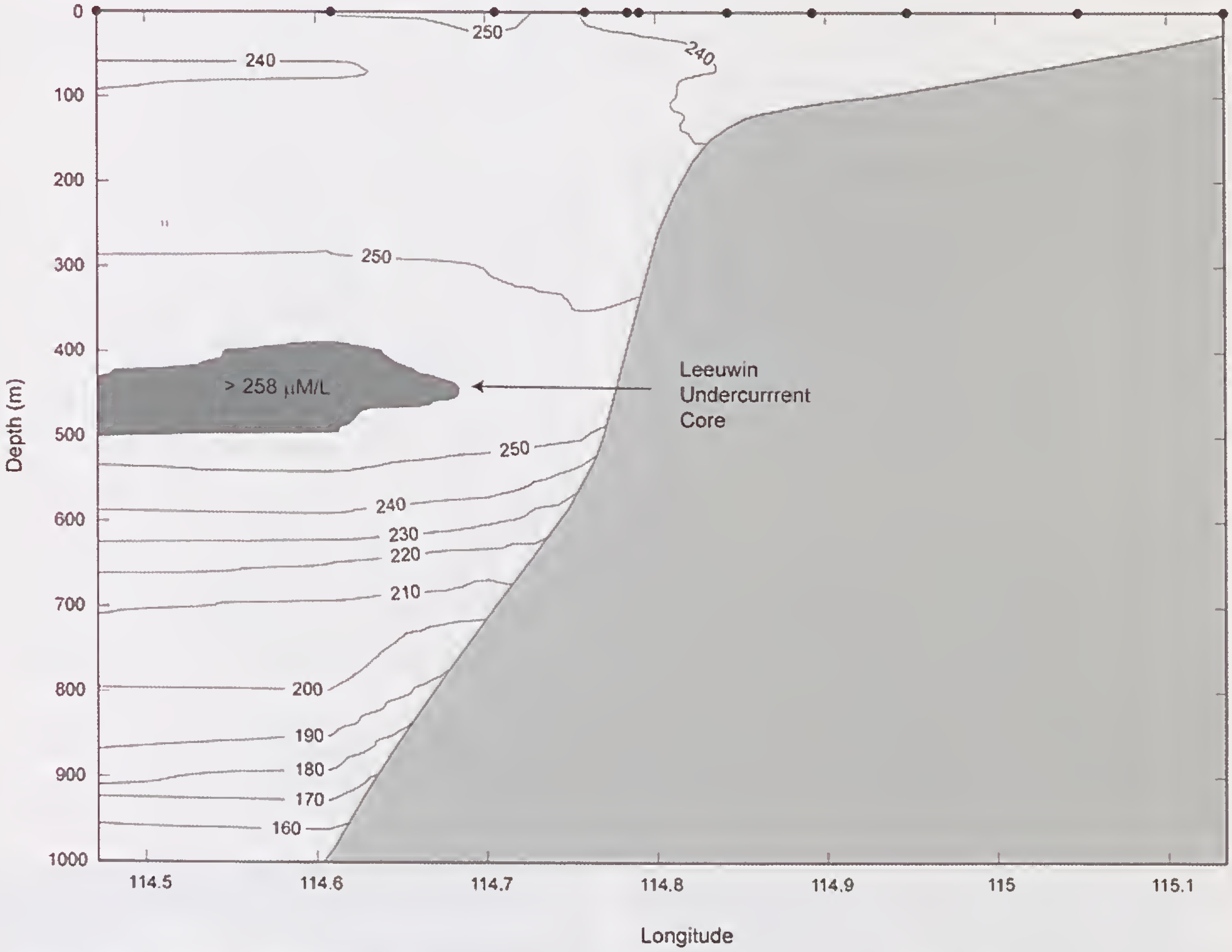

Figure 4. Cross-section of the dissolved oxygen levels for transect 6 showing the presence of the > 258-mmol/L Leeuwin undercurrent core at 450-m depth. The transect location is shown in Figure 3.

LC. Meuleners *et al.* (2007) used numerical modelling tests to estimate a geopotential gradient of 1.9×10^{-7} acting towards the equator. All the gradients listed above are a factor of 10 less than the geopotential gradient associated with the surface LC.

The LU is also associated with the subantarctic mode water (SAMW). High convection in the region to the south of Australia results in cooling which is the generation mechanism for this water mass. As it has been formed recently ('age' of the water mass is small) it has a high dissolved oxygen concentration. A cross-section of the LU core was identified from the dissolved oxygen distribution: the core of the current consisted of a dissolved oxygen maximum of 252 mM/L centred at a depth of about 450 m (Figure 4).

Several studies have shown the LU could be considered an extension of the Flinders current, which flows along the southern coast of Australian (Cirano & Middleton 2004; Akhir & Pattiaratchi 2006; Meuleners *et al.* 2007). The Flinders current is the dominant feature along the south Australian coast and extends from Tasmania to Cape Leeuwin (Cirano & Middleton 2004). A positive (anti-clockwise) wind stress curl drives the Flinders current in summer and winter, which results in northward transport (due to Sverdrup balance) centred along 135° E, which is deflected to the west to satisfy vorticity dissipation and mass conservation (Cirano & Middleton 2004).

The Flinders current is present in summer and winter, but its westward transport, which occurs between 37 and 39° S and varies between 8 and 17 Sv, is stronger during the summer (Middleton & Bye 2007). The current, which extends through the water column to a maximum depth of 800 m and reaches maximum speeds of 0.5 ms^{-1}, offshore of the shelf break, interacts with the LC at the shelf break and slope. Here, the LC is visible as an eastward flowing surface current, with the Flinders current as the westward flowing subsurface current. Comparison of Akhir and Pattiaratchi's (2006) and Meuleners *et al.*'s (2007) temperature and salinity data obtained along the south and west Australian coasts showed the Flinders current sourcing the LU core.

Because the LU is linked to the Flinders current, its seasonal and interannual variability resembles that of the

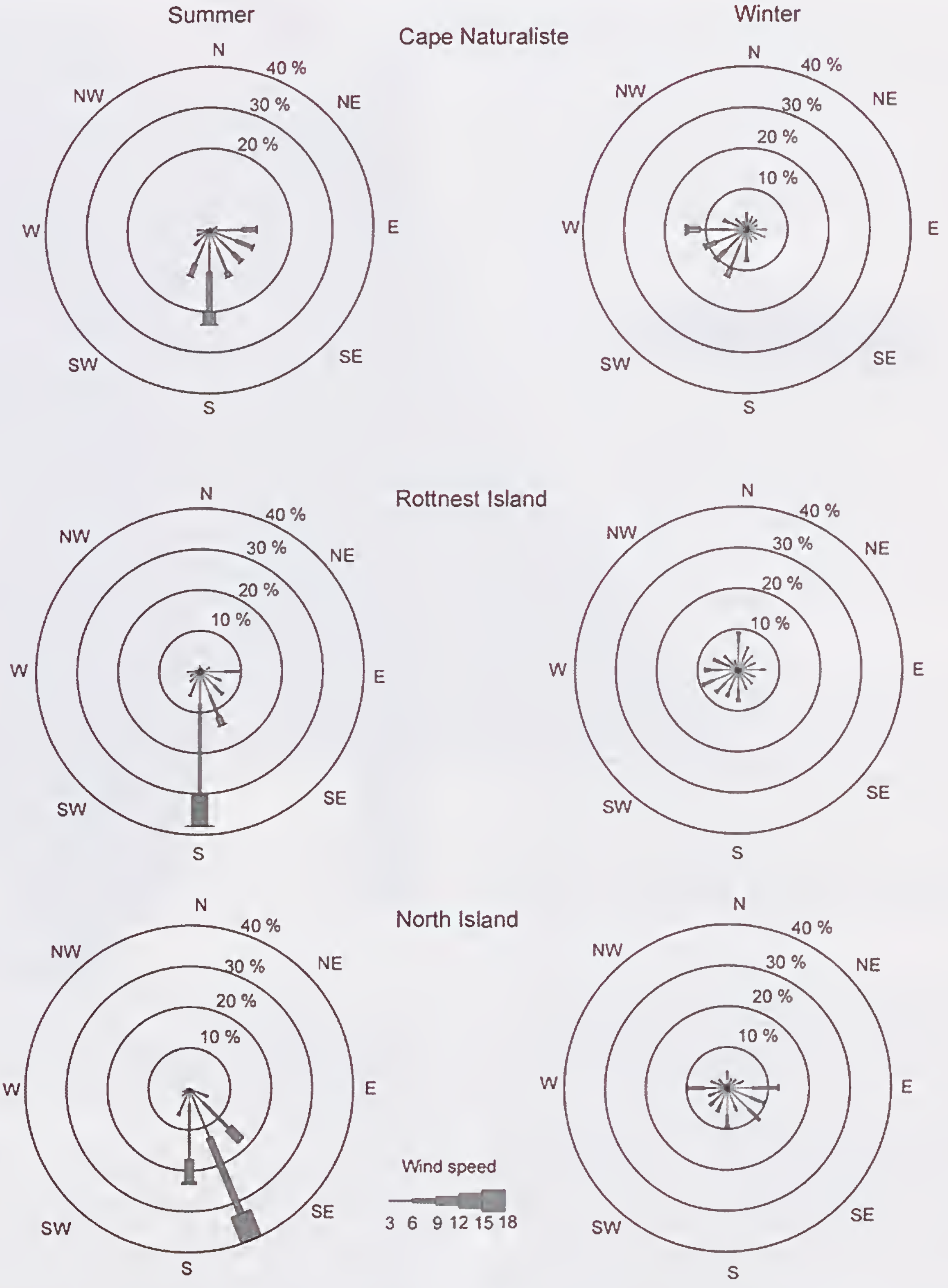

Figure 5. Summer and winter wind roses obtained from meteorological stations along the west Australian coast: Cape Naturaliste, Rottnest Island, and North Island. The station locations are shown in Figure 3.

Flinders current. Thompson (1984) and Smith *et al.* (1991) used field tests to show the LU was strongest in summer between November and January. The Flinders current is also stronger during El Niño events; thus the LU would also be stronger during El Niño events.

Continental shelf currents

Several studies have used field data and satellite imagery to examine the continental shelf circulation along the west coast of Australia in summer (Cresswell *et al.* 1989; Cresswell & Peterson 1993; Pearce & Pattiaratchi

1997, 1999; Gersbach *et al.* 1999; Hanson *et al.* 2005a, 2005b; Woo *et al.* 2006a, 2006b). These studies found a cool, northward current (the Capes and Ningaloo currents) on the continental shelf, with the southward flowing LC usually located farther offshore.

Because wind drives the continental shelf currents, the seasonal variation in the wind field off Western Australia affects the currents' behaviour. Anticyclonic high pressure systems, as well as periodic tropic and extratropical cyclones (mid-latitude depressions) and seasonal sea breezes, dominate the weather systems around south-west Australia (Eliot & Clarke 1986). Eastward moving anticyclones pass the west coast every 3 to 10 days, with the anticyclonic band migrating from ~38° S in summer (mainly causing offshore winds) to ~30° S in winter (mainly causing onshore winds) (Gentilli 1972). This seasonal movement of high pressure systems creates a strong seasonality in the wind regime along the west coast (Figure 5). In the summer, southerly winds prevail along the west coast. During the passage of a frontal system, the region is subject to strong winds (up to 25–30 ms^{-1}) from the north-west, which change direction to the west then south-west over 12–16 hours; hence there is no dominant wind direction in winter. Up to 30 storm events may occur in any given year (Lemm *et al.* 1999).

In summer, the anticyclonic belt's southerly location causes an easterly airflow over Australia. This hot airflow forms a low pressure trough in a north-south (shore-parallel) direction (Kepert & Smith 1992). This pressure trough, which is usually located inland, produces the prevailing southerly winds on the west Australian coast.

The combination of the sea breeze (south-westerly airflow) and the synoptic conditions (south-easterly airflow) causes a southerly sea breeze, which blows parallel to the shore, unlike the 'classic' sea breeze where the winds blow perpendicular to the shore. The sea breeze onset is rapid, with initially high velocities, and the surface currents respond almost instantly (Pattiaratchi *et al.* 1997). Masselink and Pattiaratchi (2001) examined wind fields at meteorological stations along the west Australian coast over a 40-year period. They found that about 200 sea breezes occurred annually, with wind speeds in the summer often exceeding 10 ms^{-1}. These strong, southerly winds dominated the continental shelf region in summer and drove the Capes and Ningaloo currents.

The Capes current

Seasonal flow reversals on the continental shelf offshore Rottnest Island was first reported by Rochford (1969) through the examination of annual salinity cycle and through the use of drift cards. Rochford (1969) found that there was a northward drift of higher salinity water during the summer months. Pearce and Pattiaratchi (1999) defined the Capes current as a cool, inner shelf current, which originated from the region between Capes Leeuwin and Naturaliste (i.e. 34° S) and moved equatorward along the south-west Australian coast in summer (Figure 6). Woo *et al.* (2006b) used field data to

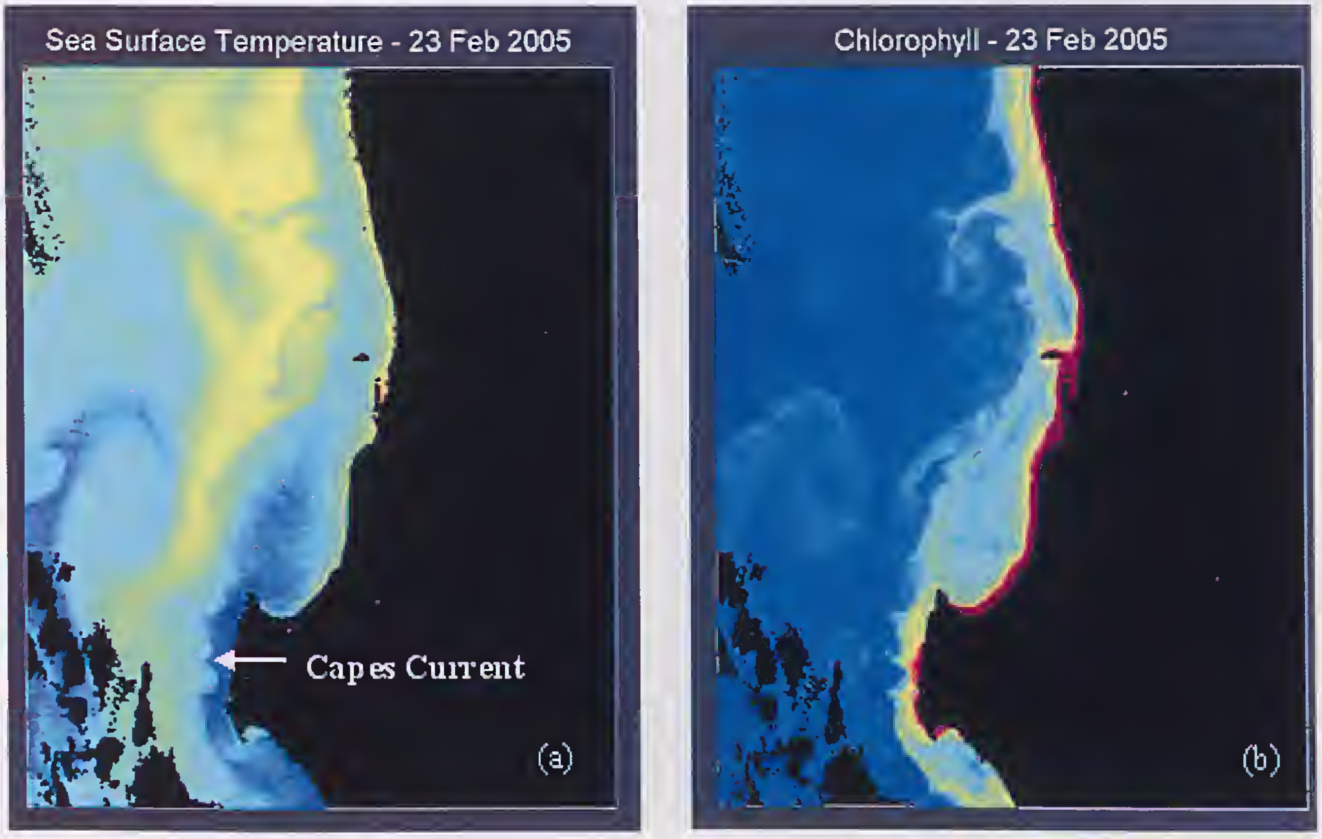
Sea Surface Temperature - 23 Feb 2005
Capes Current
(a)
Chlorophyll - 23 Feb 2005
(b)

Figure 6. Ocean colour satellite images of the region offshore south-west Australia obtained with the MODIS (moderate resolution imaging spectroradiometer) on 23 February 2005 showing the sea surface temperature and the upwelling of cold water into the Capes current (a) and the associated high chlorophyll concentration (b).

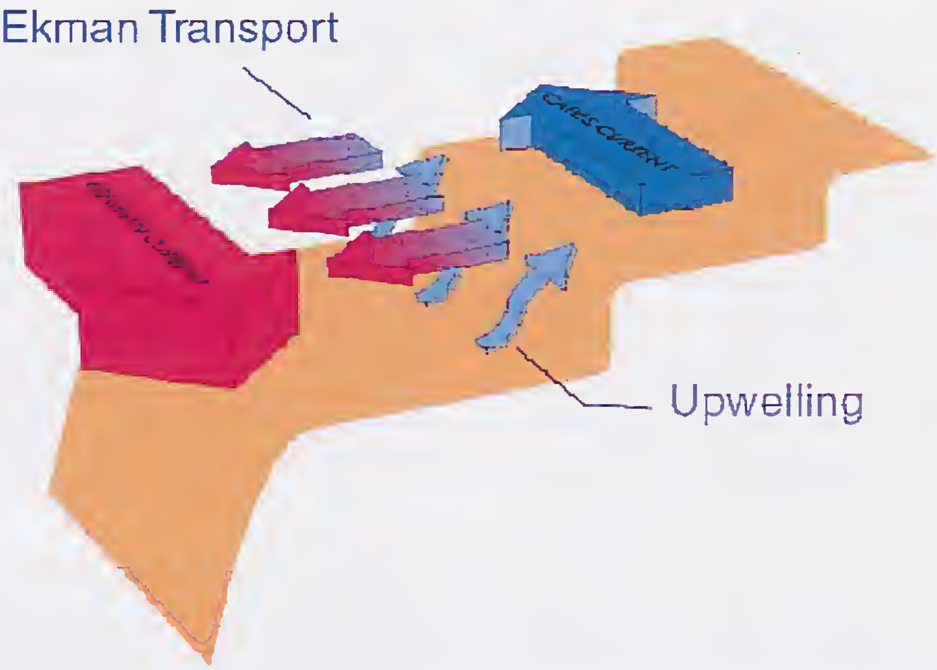

Figure 7. Cross-sectional schematic of the steady-state current regime off south-west Australia in summer (from Gersbach *et al.* 1999).

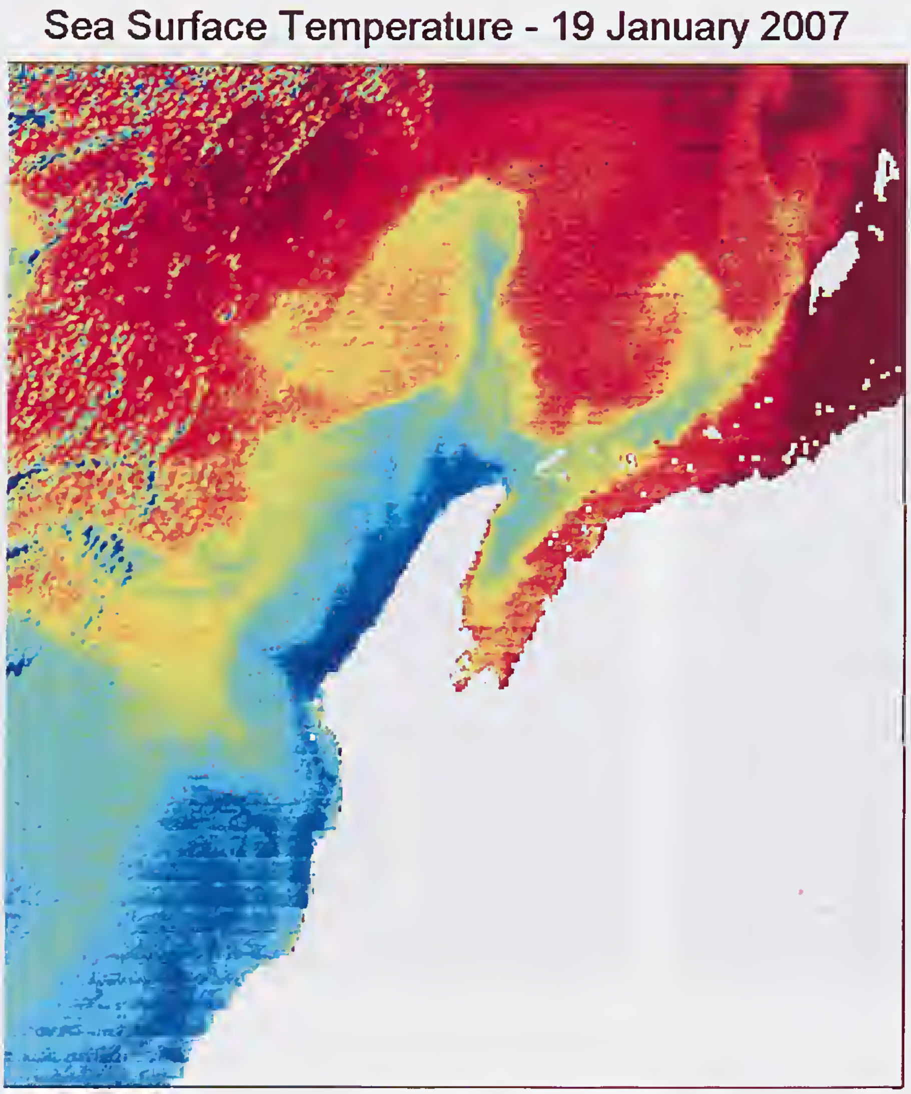

Figure 8. MODIS-derived satellite sea surface temperature image of the Ningaloo current obtained on 19 January 2007.

confirm the Capes current extended as far north as the Abrolhos Islands (32° S). The current has a salinity content of 35.37–35.53 and a temperature of 21.0–21.4 °C, which is cooler than the LC.

Several studies have found the Capes current is sourced from water upwelled from the bottom of the LC (at ~100-m depth), which usually occurs between Capes Leeuwin and Naturaliste, and also from water from the south (to the east of Cape Leeuwin) (Gersbach *et al.* 1999; Pearce & Pattiaratchi 1999; Hanson *et al.* 2005a). The Capes current is well established by November when the winds in the region are mainly southerly because of the strong sea breezes (Pattiaratchi *et al.* 1997) and continues until about March when the sea breezes weaken.

Gersbach *et al.* (1999) described the dynamics of the Capes current off Cape Mentelle in their study on upwelling along the south-west Australian coast. Here the southerly wind stress overcame the alongshore pressure gradient, which pushed the surface waters and the LC farther offshore and upwelled cold water onto the continental shelf (Figure 7). Gersbach *et al.* (1999) also used numerical modelling to show that a wind speed of 8 ms^{-1} was enough to overcome the alongshore pressure gradient on the inner continental shelf.

The Ningaloo current

The Ningaloo current flows north along the inner continental shelf between the LC and the coast. A strong, southerly wind stress drives the current (Taylor & Pearce 1999; Woo *et al.* 2006a), similar to the Capes current along the south-west Australian coast. Taylor and Pearce (1999) used aerial surveys and satellite imagery to observe the Ningaloo current moving north along the Ningaloo reef front, forming a distinct line in the water and separating the coastal waters from the southward flowing LC some 2 km offshore. Studies using field data (Hanson *et al.* 2005b; Woo *et al.* 2006b) and numerical modelling (Woo *et al.* 2006a) found the Ningaloo current inshore of the 50-m isobath, extending from Shark Bay (Figure 2) to North West Cape and beyond.

At Point Cloates (Figure 2), under low wind conditions, the current splits and forms an anticyclonic circulation pattern to the south-west (Figure 8; part of the current moves across the shelf to flow south, parallel to the coast. The LC water is taken northward adjacent to the Ningaloo reef, in the Ningaloo Current (Woo *et al.* 2006a). Woo *et al.*'s (2006b) field data showed the Ningaloo current consisted of colder (< 23 °C), more saline (34.92) water than the offshore waters and had a similar temperature–salinity signature to the LC. Hanson *et al.* (2005a) recorded upsloping isotherms in their temperature contour plots of the region off south-west Australia, which showed upwelling had occurred off North West Cape. They also found the Ningaloo current had high nutrient concentrations and phytoplankton biomass and maximum regional primary production rates.

Shark Bay outflow

Shark Bay is a coastal, semi-enclosed embayment with deep, open waters to the north and two shallow gulfs to the south, bounded by three large islands to the west (Figure 2). Nahas *et al.* (2005) found a two-layered flow of seawater in the Geographe and Naturaliste channels, with the less dense, low salinity water flowing into the bay at the surface and the high density, high salinity water exiting the Bay near the seabed (Figure 9). James *et al.* (1999) proposed that a plume of high salinity water flowed south on the continental shelf near the seabed. Woo *et al.* (2006b) used a temperature–salinity diagram to show the outflow water had a high salinity. We identified the high salinity water from Shark Bay as a distinct water mass on the continental shelf with a temperature ranging between 21.2 and 22.9° C and salinity up to 36.1.

Localised flow associated with topographic features: the Perth Canyon

The interaction between shelf and slope current systems causes localised flow patterns, which affect the ecology in the canyon vicinity. Compared with their surroundings, submarine canyons have higher biodiversity and biological productivity (Hickey 1995), which is often attributed to upwelling at the canyon

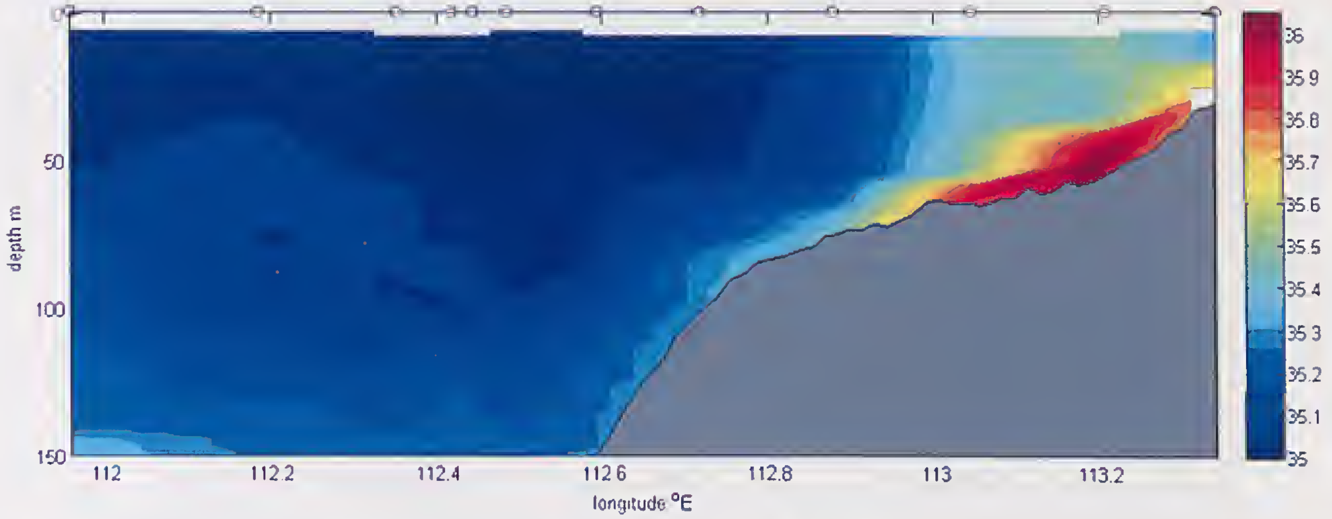

Figure 9. Cross-sectional transect of the region offshore Shark Bay showing the high salinity outflow of water onto the continental shelf.

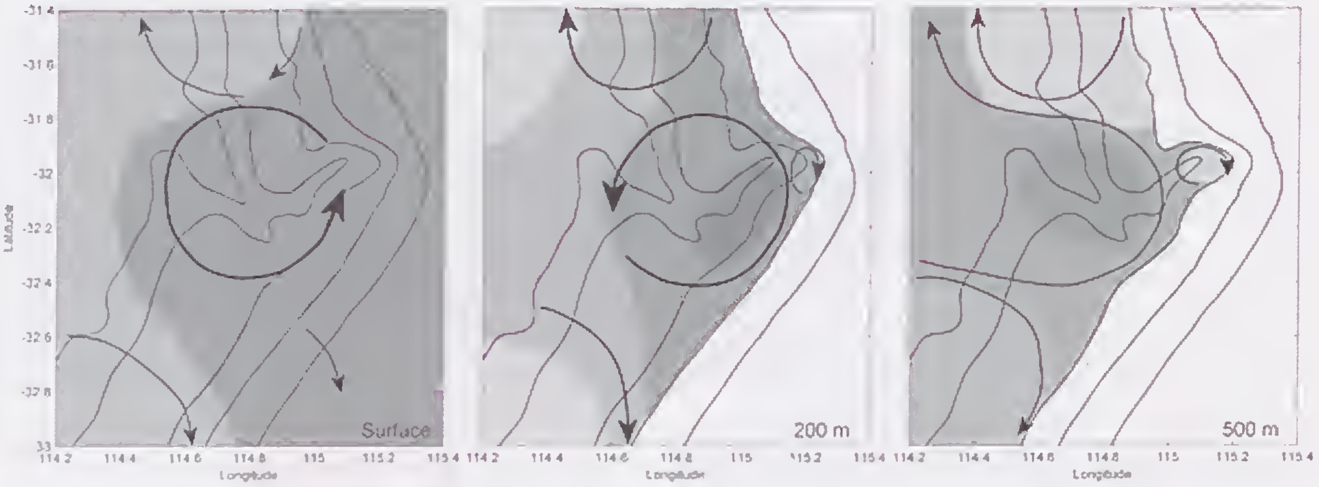

Figure 10. Water flow patterns in the Perth Canyon at the surface, 200-m, and 500-m depths. The shading indicates the temperature, with the lighter shades (colder temperature) showing the upwelling regions (from Rennie *et al.* 2009).

enriching the photic zone with nutrients. The Perth Canyon is an extension of the Swan River system within the Mentelle sub-basin, which cuts into the continental shelf west of Perth and Rottnest Island. The canyon starts at the 50-m contour and is ~100-km long and ~10-km wide near its head. It is 3-km-deep at the shelf slope and cuts 4-km-deep into the continental slope. At the canyon head, the depth plunges from 200 to 1000 m, with the canyon mouth opening onto the abyssal plain at a depth of 4000 m. Hence the Perth Canyon can be described as long, deep, narrow, steep-sided and intruding into the continental shelf.

Rennie *et al.* (2009) found that the LU interacting with the canyon generated eddies within the canyon (Figure 10). These clockwise eddies, which were formed over five to ten days and favoured upwelling at their centre, would then migrate farther offshore. Eddies sometimes recurred within the canyon, which suggested the canyon regulated the circulation, with several circular eddies of different sizes and depths present in the canyon at any given time. These circulation patterns enabled the canyon to support high levels of primary and secondary production; indeed the canyon was a feeding area for pygmy blue whales during the summer (Rennie *et al.* 2006).

Eddies caused regions of upwelling or downwelling, with deep upwelling stronger in the canyon than elsewhere on the shelf. Near-surface vertical transport was strong everywhere when wind forcing was present. The circulation in the canyon produced upwelling to above 300-m depth, mainly at the head and along the canyon rims, but also contributed to downwelling. Rennie *et al.*'s (2007) model results suggested upwelling at the canyon head occurred when a clockwise surface eddy was centred over the south rim, whereas an eddy (either clockwise or anticlockwise) centred on the north rim caused net downwelling.

Increased upwelling, combined with strong, upwelling-favourable winds and the entrapment of eddies within the canyon, increased the primary productivity in the canyon; however, the LC formed a strong barrier to water upwelling to the surface. Because the canyon rims are deep, upwelling alone was insufficient to transport nutrients to the euphotic zone.

Surface and subsurface water masses

Temperature data from bathythermographs and CTDs (conductivity, temperature, and depth) sensors can reveal the general structure of a water column. Off the west Australian coast, turbulent mixing, e.g. by surface wind stress, and the presence of the LC produce a well-mixed layer at the surface. The well-mixed layer is deeper within the LC than it is onshore or farther offshore. The mixed-layer depth, which can be greater than 100 m, varies with the season and El Niño – southern oscillation events (Feng *et al.* 2003). Below the well-mixed layer, the thermocline usually descends to around 400-m depth,

Table 1

Characteristics of the water masses found at the 1000-m isobath along the west Australian coast.

Water mass	Temperature (°C)	Salinity	Dissolved oxygen (iM/L)
Tropical surface water (TSW)	22–24.5	34.7–35.1	200–220
South Indian central water (SICW)	12–22	35.1–35.9	220–245
Subantarctic mode water (SAMW)	8.5–12	34.6–35.1	245–255
Antarctic intermediate water (AAIW)	4.5–8.5	34.4–34.6	115–245
North-west Indian intermediate (NWII) water	5.5–6.5	~34.6	100–110
Circumpolar deep water (CDW)	2–3.8	34.57–34.75	120–200
Antarctic bottom water (AABW)	0.8–1.8	~34.71	~210

although sub-layers may exist in this depth range. The sea surface temperature cools in the austral winter and warms in the austral summer, with the deepest mixed-layer depths occurring in winter (Hamilton 1986; Feng *et al.* 2003).

Woo and Pattiaratchi (2008) identified five water mass types in the upper Indian Ocean (< 1000-m depth) along the west Australian coast (see Table 1), which corresponded with classical water masses of the Indian Ocean (Wyrtki 1971; Warren 1981). Two other water masses—circumpolar deep water (CDW) and Antarctic bottom water (AABW)—were also present in the deeper waters. Woo and Pattiaratchi (2008) observed all these water masses in the vertical distribution of salinity and dissolved oxygen as interleaving layers of salinity and dissolved oxygen (Figures 11 and 12).

In order of increasing depth, these water masses were:

(i) low salinity tropical surface water (TSW)

(ii) high salinity south Indian central water (SICW)

(iii) high oxygen subantarctic mode water (SAMW)

(iv) low salinity Antarctic intermediate water (AAIW)

(v) low oxygen north-west Indian intermediate (NWII) water

(vi) low oxygen upper circumpolar deep water (UCDW)

(vii) high salinity lower circumpolar deep water (LCDW)

(viii) cold (< 2 °C), high oxygen Antarctic bottom water (AABW).

Temperature, salinity and dissolved oxygen were measured to locate the above water masses and their positions relative to each other along the whole coast from North West Cape (21° S) to Cape Leeuwin (35° S) (Figure 12). In the following sections, we summarise the characteristics of each of the above water masses.

Tropical surface water (TSW)—salinity minimum

A layer of low salinity (< 35.1), warm (> 22°C) tropical water found in the surface water in the northern region between North West Cape and the Abrolhos Islands), corresponded with the temperature/salinity characteristics of the Leeuwin Current water. This water mass was derived from the Australasian Mediterranean water, a tropical water mass with origins in the Pacific Ocean central water and formed during transit through the Indonesian archipelago (Tomczak & Godfrey, 1994). At the North West Cape (21 °S), the northern extent of the study region, this water mass extended to 180 m and exhibited a surface salinity of less than 34.9 (Figure 12). With the southward passage of the Leeuwin Current, the water mass shallowed and disappeared at ~26 °S. The salinity signature (which was < 35.1) disappeared because of the entrainment of cooler, saltier south Indian central water (see below) from offshore due to eddy activity and geostrophic inflow (Woo *et al.*, 2006b).

South Indian central water (SICW)—salinity maximum

South Indian central water (SICW) was identified here as a salinity maximum layer (35.1–35.9). Along the 1000-m bathymetric contour, shipborne ADCP (acoustic Doppler current profiler) data revealed the SICW's core moving northward at a maximum speed of 0.3 ms^{-1} along the 26.8 density (s_t) level. However, near the shelf break this same water mass was part of the Leeuwin Current flowing southwards (Woo *et al.*, 2006b). Here, ADCP data indicated that the Leeuwin Current extended up to 300-m water depth, which was the total depth of the SICW (Figure 12). SICW had a temperature range of 12–22°C and was associated with weak minima of dissolved nitrate, silica, and phosphate. South of 29.0 °S, SICW was found at the surface. But northward of 29.0 °S, the salinity maximum gradually subducted beneath TSW, reaching a depth of 245 m at 21.5°S.

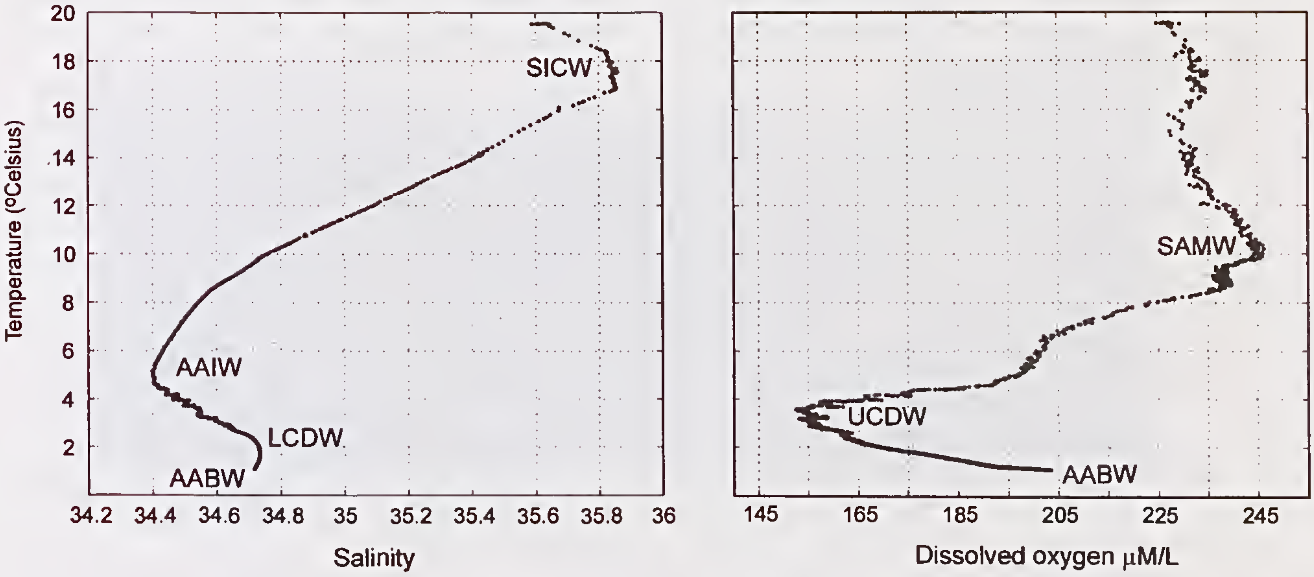

Figure 11. The temperature–salinity and temperature – dissolved oxygen diagrams for the Perth Basin showing the water masses off the west Australian coast. Station location is shown on Figure 2.

Subantarctic mode water (SAMW)—oxygen maximum

Beneath the south Indian central water (SICW), a water mass with high dissolved oxygen concentrations of 245–255 μM/L was identified as subantarctic mode water (SAMW) whose core occurred at 400–510 m (Figure 12). SAMW consisted of water with a temperature range of 8.5°–12°C and salinity range of 34.6–35.1. SAMW is formed by deep winter convection at 40°–50°S in the zone between the subtropical convergence and the Subantarctic Front to the south of Australia (Wong, 2005). As SAMW is formed by deep convection rather than subduction, newly formed SAMW penetrates to a greater depth than the newly subducted SICW (thus, is comparatively better ventilated) and then moves northward from its formation region. Due to its high oxygen content, the SAMW plays an important role in ventilating the lower thermocline of the southern hemisphere subtropical gyres (McCartney, 1982). High oxygen content found in the core of the LU shows that the LU comprises of SAMW (Figure 4).

Antarctic intermediate water (AAIW)—salinity minimum

Below the SAMW, a salinity minimum (34.4–34.6) was observed, indicating the presence of Antarctic intermediate water (AAIW) along the coast (Figure 12). The water was cold (4.5°–8°C) and the position of its core became shallower northward (the core depth was 875 m at 27.5°S and 520 m at 21.5°S). It has been reported the AAIW extends northward from the Antarctic Polar Front to latitudes 10°–15°S, and is thought to flow more slowly than the oxygen maximum layer above it (Warren, 1981).

Northwest Indian intermediate (NWII) water—oxygen minimum

An oxygen minimum signature of < 110 μM/L in the northern region (21.3°–24.5°S) indicated the presence of northwest Indian intermediate (NWII) water immediately beneath the AAIW (Figure 12). This water mass originated from the Red Sea and Persian Gulf outflows. Occupying depths of 800–1175 m, the temperature of the NWII water was < 5°C and its salinity ranged between 34.55 and 34.65. NWII water was associated with maxima of dissolved nitrate, silica and phosphate.

Upper circumpolar deep water (UCDW) and lower circumpolar deep water (LCDW)

In the southern region (between the Abrolhos Islands and Cape Leeuwin), a water mass with similar characteristics to NWII water was found below the AAIW

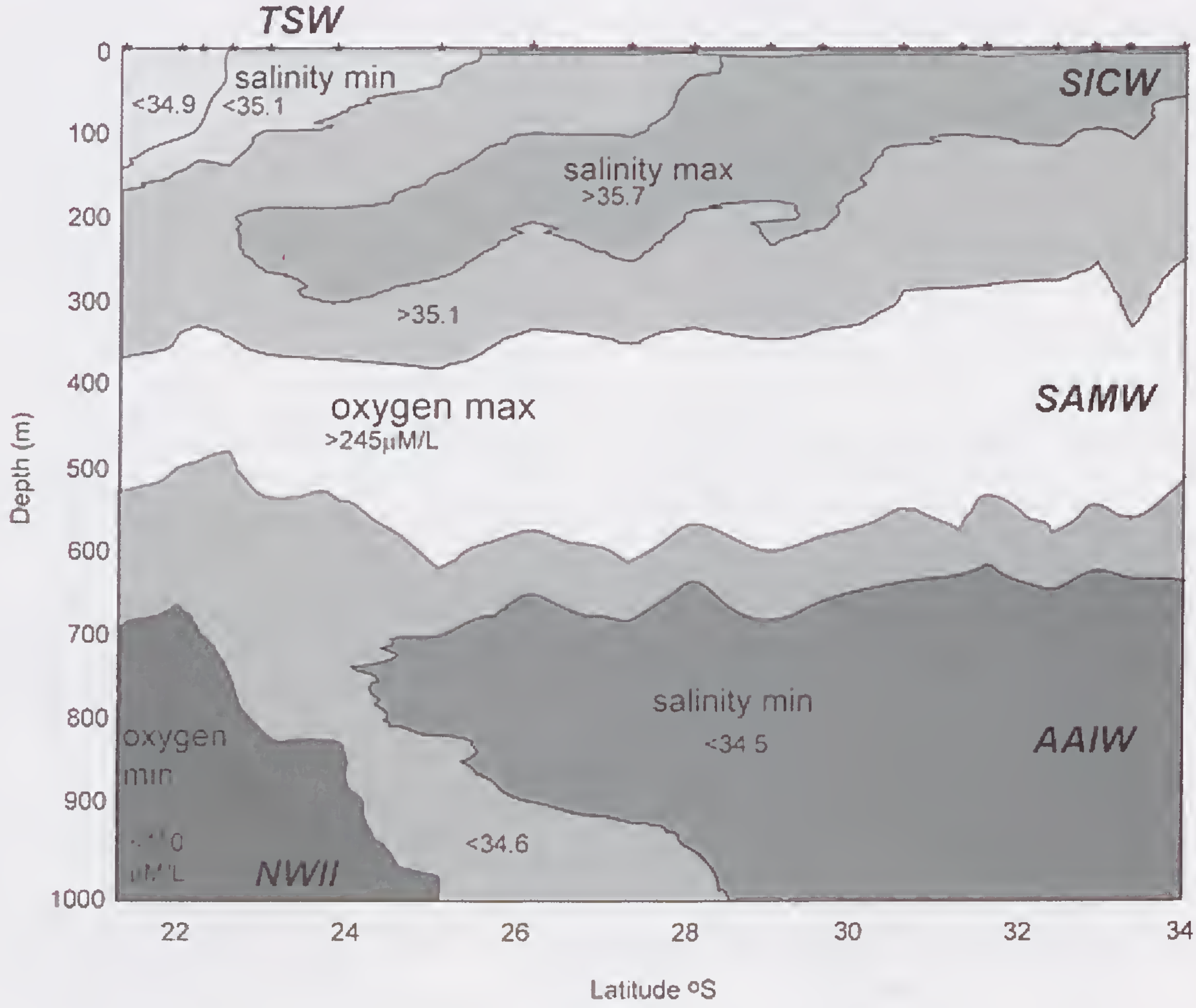

Figure 12. The main water masses observed at a section along the 1000-m isobath, parallel to the west Australian coast (modified from Woo & Pattiaratchi 2008).

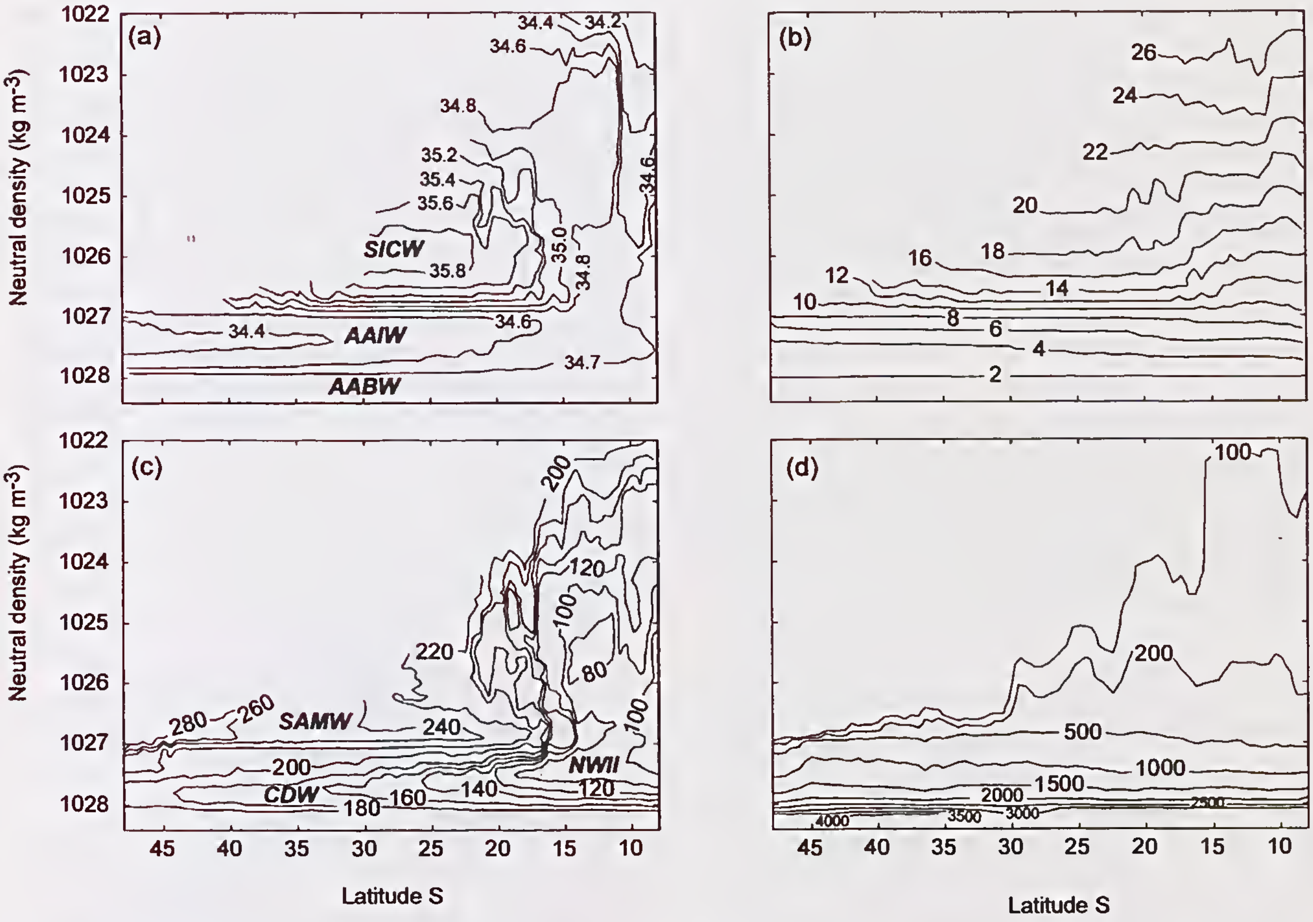

Figure 13. The isopleths of salinity (a), temperature (in degrees Celsius) (b), dissolved oxygen concentration (in M/L) (c), and depth (in metres) (d) plotted against neutral density (kg/m^3). The data for the region south of 35° S were obtained from voyage FR10/1994 (along 120° E), and the data for the region north of 34° S were obtained from voyage FR09/2000 (along 95° E).

and identified as circumpolar Deep Water (CDW). The CDW could be separated into two distinct water masses: lower circumpolar deep water (LCDW) and upper circumpolar deep water (UCDW) (Figure 11).

Lower Circumpolar Deep Water (LCDW) directly overlaid AABW (see below). It was characterised by a salinity maximum reaching 34.75 in the south and 34.72 in the north (Figure 13a). This water mass has also been referred to as Indian deep water (IDW) and upper deep water (Tomczak & Godfrey 1994). The high salinity content in LCDW is formed by North Atlantic Deep Water (NADW) being injected into the Antarctic Circumpolar Current (ACC) (Whitworth *et al.* 1998; Fieux *et al.* 2005), and then gradually getting modified along its course through constant mixing with deep waters during its eastward journey in the ACC (Tomczak & Liefrink 2005). LCDW moved along the 28.07kg/m^3 neutral density surface. Its oxygen content decreased from >200ìM/L in the south to 170ìM/L in the north, thus indicating northward motion (Figure 13c). LCDW maintained potential temperature of around 1.5°C in a depth range of 2600–3100m (Figure 13b).

Upper circumpolar deep water (UCDW), which occurred just beneath Antarctic intermediate water (AAIW), was characterised by an oxygen minimum (Tomczak & Liefrink 2005). UCDW was observed flowing at depths of around 1550 m on a neutral density surface of 27.8 kg/m^{-3}, with its oxygen concentration decreasing from 180 ìM/L in the south to 120 ìM/L in the north (Figure 13c). Potential temperatures and salinities both increased northward, from 2.6°C/ 34.57 to 3.6°C/34.75 respectively.

Antarctic bottom water (AABW)

Antarctic bottom water (AABW) is one of the densest water mass found in the World Ocean (Tomczak & Liefrink 2005). AABW flows onto the West Australian Basin, forming a western boundary current along the Ninety East Ridge (Tomczak & Godfrey 1994). As the area of the 28.2 kg/m^3 neutral density surface is limited to the southern part of the Perth Basin, AABW must upwell (Sloyan 2006). Indeed, the continuity of AABW into the West Australian Basin was clearly detected in deep CTD records (>4000 m depth) taken in the West Australian Basin. Across 8°S where data was sampled down to 5000m (28.18 kg/m^3 neutral density), the bottom water exhibited a salinity of 34.71, potential temperature of 0.6°C and dissolved oxygen concentration of 210ìM/L, which is typical of AABW in these basins.

Recent observations of the Leeuwin current system

The CTD data of the Leeuwin current system obtained during the Leeuwin Current Interdisciplinary Experiment (1987–1988) (Church *et al.* 1989; Smith *et al.* 1991) supplemented Rochford's (1969) and Thompson's (1984) studies of the LC. Cresswell and Peterson (1993) also used CTD and ADCP measurements to study the LC off south-west Australia. Recent studies of the LC include those of Fieux *et al.* (2005) and Woo *et al.* (2006b). Woo *et al.* (2006b) used the research vessel ORV *Franklin* (voyage no. FR10/2000) to study the oceanographic processes along the continental shelf and slope between North West Cape and the Abrolhos Islands (referred to here as the northern region) in November 2000. Twomey *et al.* (2007) used the RV *Southern Surveyor* (voyage no. SS06/2003) to study the phytoplankton–nitrogen dynamics across the continental shelf between the Abrolhos Islands and Cape Leeuwin (referred to here as the southern region) in November 2003. Here we summarise the results obtained from both regions.

The two voyages took place in the early austral summer (October/November) of 2000 and 2003. Between 13 and 27 November 2000, eleven cross-shelf transects were obtained between 21 and 28° S in the northern region (Figure 2); between 24 October and 9 November 2003, fourteen cross-shelf transects were obtained between 28 and 35° S in the southern region (Figure 2). The instruments deployed included a Neil Brown CTD recorder (FR10/2000) and a Sea-Bird CTD sensor (SS06/2003), each with a 24 x 5-L bottle on a Niskin rosette (for calibration and water sampling), a 150-kHz RDI acoustic Doppler current profiler (ADCP) linked to the global positioning system, a Turner Designs fluorometer, a near-surface thermosalinograph, and meteorological sensors. On both voyages, the cross-shelf stations extended from 50 to 1000-m water depths. Depending on the continental shelf width, 10–15 stations were occupied at the 50-m, 100-m, 150-m, 200-m, 250-m, 300-m, 500-m, 750-m, and 1000-m depth contours. Note that these studies occurred in the late spring and early summer when the LC is usually weaker.

North West Cape to the Abrolhos Islands

Woo *et al.* (2006b) studied the region between North West Cape and the Abrolhos Islands and found it comprised four different water masses (Figures 14 and 15). Offshore eddies, wind stress, varying shelf widths, the coastal topography, and outflow from the hypersaline Shark Bay all affected this complex current system. Hanson *et al.* (2005b) also studied this region off the west

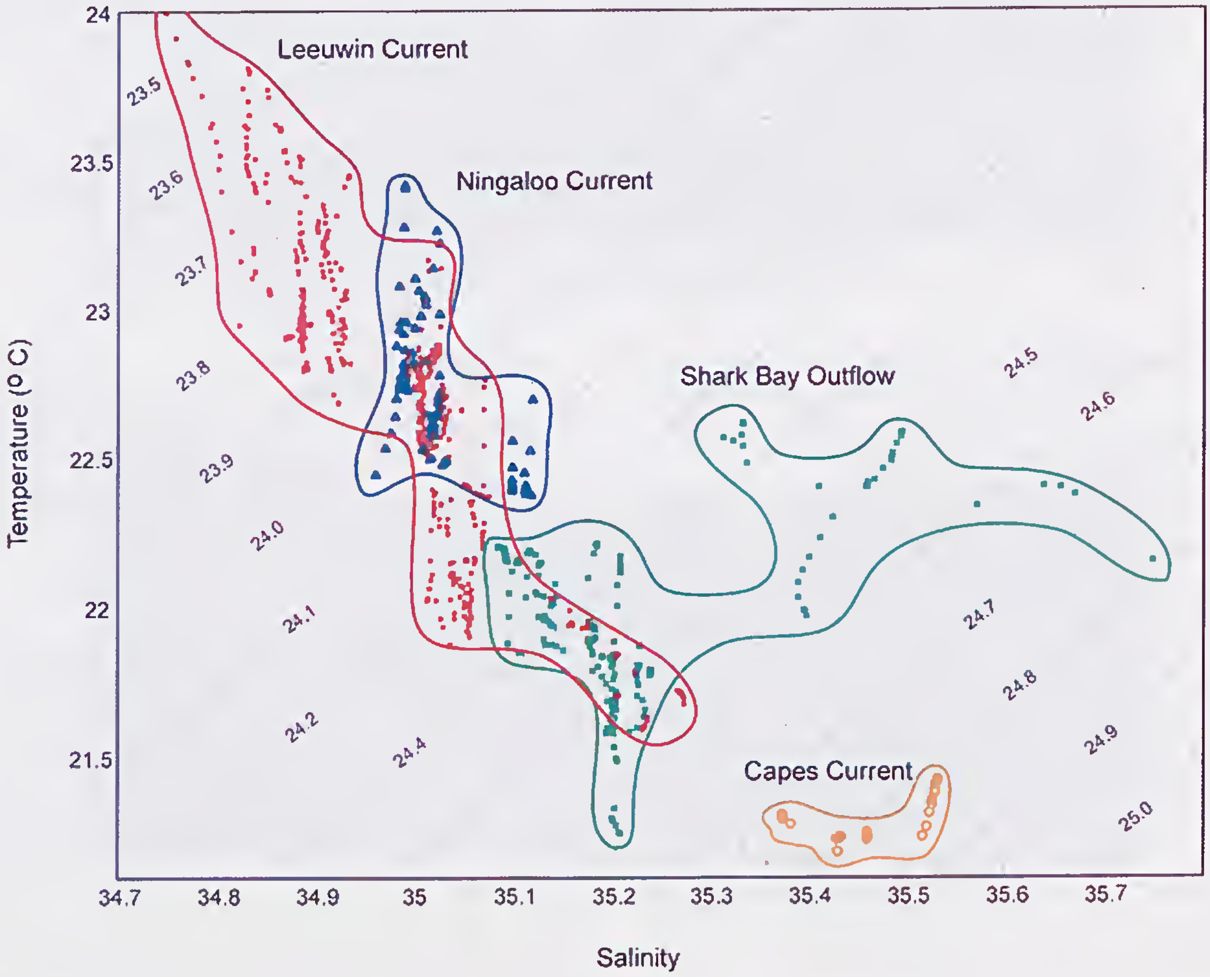

Figure 14. The temperature–salinity diagram of the surface water layer (top 100 m) from the coast to the 1000-m isobath in the northern region of the study area showing the presence of four different water masses (modified from Woo *et al.* 2006b).

Australian coast; however, they focused on the phytoplankton response to small-scale upwelling.

The LC transported warm, low salinity water poleward along the 200-m isobath. In the north, the LC water was warm (24.7 °C) and had a low salinity (34.6). As the current moved south, the geostrophic inflow of offshore waters cooled the LC water to 21.9 °C and increased its salinity to 35.2 (Figure 14).

The width and depth of the current also changed in response to the changing bottom topography and the coastline orientation. In the northern region, the narrow shelf and steep slope strengthened the current (recorded velocity of ~0.75 ms^{-1}) and pushed it deep into the water column. In contrast, the current decelerated to ~0.2–0.4 ms^{-1} as it flowed past the wide continental shelf offshore Shark Bay and then accelerated in the southern region as it flowed along the steep continental slope. Changes in the shelf width at Point Cloates also split the northward moving Ningaloo current (Figure 15).

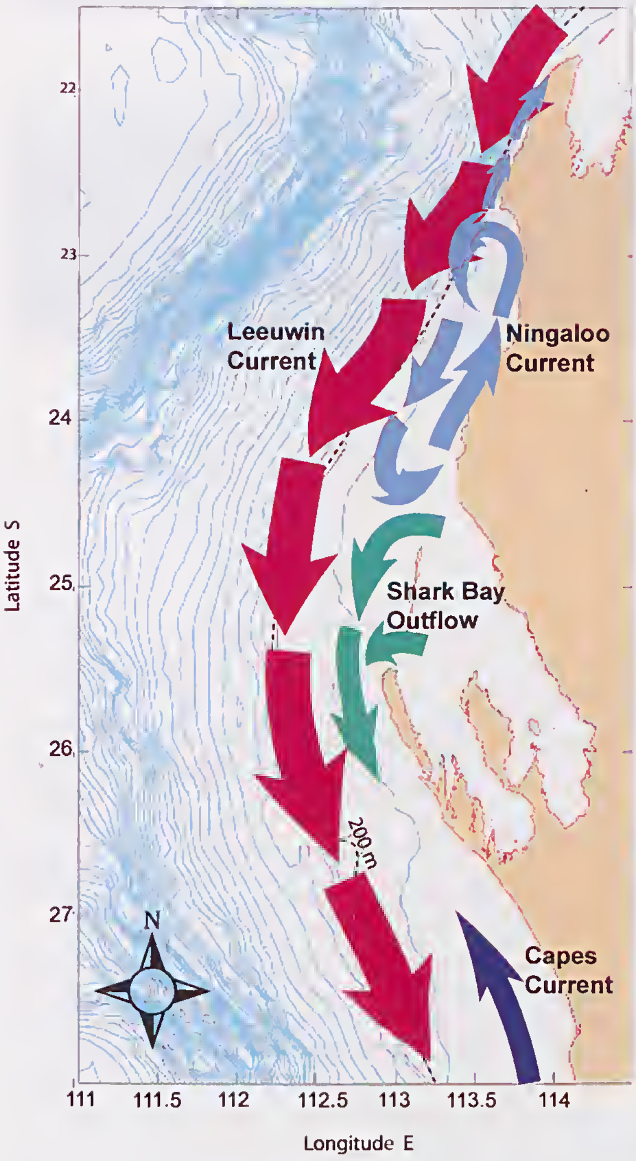

Figure 15. Schematic of the surface circulation in the northern region of the study area based on field data collected aboard the ORV *Franklin* (from Woo *et al*. 2006b).

Downwelling events were usually associated with the current. The Ningaloo current was confined to the north Gascoyne shelf within 35 km of the coast. Although upwelling was detected in the northern region, adjacent to the Ningaloo coral reef, the water properties suggested the LC water was recirculated from the south (Figure 14). In the continental shelf region to the west of the main bay entrances, the high salinity outflow water mixed with the shelf waters. The Capes current, a wind-driven current originating from the south of the study region, was identified as a cool, high salinity water mass flowing north.

The Abrolhos Islands to Cape Leeuwin

The voyage was completed over a period of 17 days and the CTD transects (Figure 2) were undertaken from north to south. At the beginning of the voyage, the winds were weak and gradually increased to speeds > 8ms^{-1} and from a southerly direction (see Figure 5d; Hanson *et al*., 2005b). Thus, the northerly transects were undertaken under low wind conditions whilst the southerly transects were undertaken during strong southerly (upwelling favourable) winds.

The cross-shelf CTD and ADCP transects provided detailed information on the LC's cross-sectional structure and the changes the LC underwent as the LC moved through the study region. For example, Figure 16 shows that at transect 2, the LC core at the surface was warmer (recorded temperature of ~20 °C) than the surrounding water, had a low salinity (~35.55), flowed poleward with speeds of > 0.60 ms^{-1}, and extended to a depth of ~250 m (the ADCP's maximum depth limit). The steep continental slope and the changes in the shoreline orientation caused the LC to accelerate in this region (Woo *et al*. 2006b; Meuleners *et al*. 2007). On the continental shelf, the current flowed north but was weak (recorded speed of ~0.10 ms^{-1}) because of the weak winds. The temperature and salinity isopleths beneath the LC were also depressed, which suggested downwelling had occurred.

Figure 17 shows that at transect 12, the LC core was warm but had a higher salinity content than the LC core at transect 2. The LC's surface salinity had increased to > 35.75; its temperature had decreased to 18 °C; its speed had decreased to ~0.20 ms^{-1}; and its core was located farther offshore. Upwelling had occurred on the continental shelf, and strong, northward currents (> 0.30 ms^{-1}) indicated the presence of the Capes current. These findings agreed with Gersbach *et al*.'s (1999) observations that southerly winds with speeds > 8 ms^{-1} overcame the alongshore pressure gradient, pushed the surface waters and the LC farther offshore, and upwelled cold water onto the continental shelf (Figure 7).

Comparison of the northern and southern regions

The ORV *Franklin* and RV *Southern Surveyor* CTD data obtained at the 1000-m depth contour were used to build a pseudo-CTD transect line (Figure 18). Note that the transects for both voyages were obtained at around the same time of year (October/November) and thus showed an interannual variability. The southernmost transect of the ORV *Franklin* voyage was also used as the northernmost transect of the RV *Southern Surveyor*

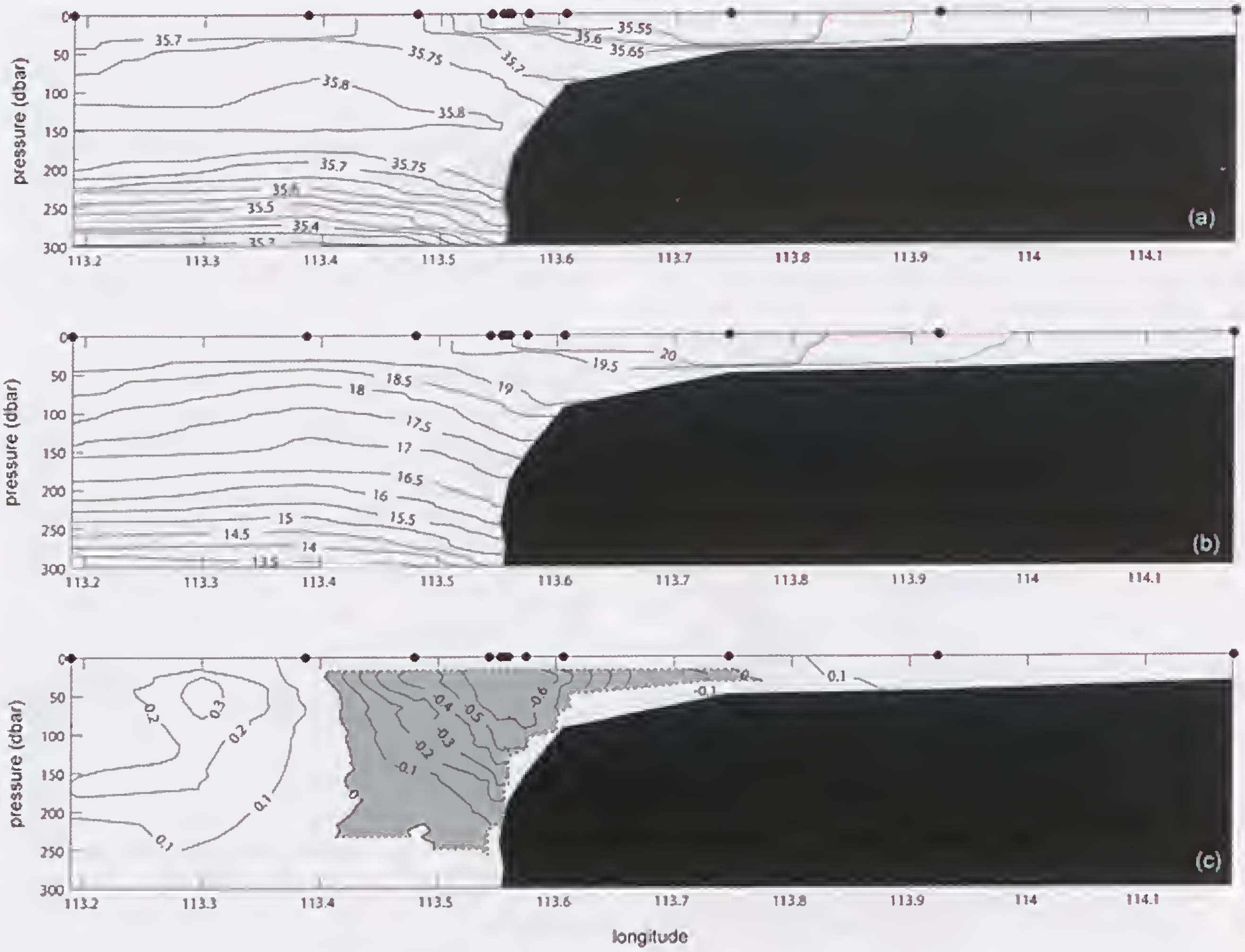

Figure 16. Transect 2 cross-sections (to 300-m depth) of salinity (a), temperature (b), and alongshore velocity (c) obtained with the ADCP. The shaded region in (c) indicates a poleward flow.

voyage. The data obtained at the 1000-m depth contour (Figure 18) showed the surface water temperature had decreased by ~1 °C (from 21 to 20 °C) and the salinity had increased by 0.3 (from 35.3 to 35.6) between November 2000 and October/November 2003. These changes in the surface water were most likely due to the LC weakening between 2000, a La Niña year, and 2003, and supported Feng *et al.*'s (2003) findings that the LC was stronger during La Niña events than it was during El Niño events.

Woo *et al.* (2006b) found that mixing changed the LC's temperature and salinity as the LC moved south—a process known as 'ageing'. The LC was warm (recorded temperature of 24 °C) with a salinity of 34.7 at the northern end of the transect (21° S). At the southern end of the transect (35° S), the water had cooled to 17.5 °C and its salinity had increased to 35.7 (Figure 18). Evaporation and atmospheric cooling would have contributed to these changes in the LC's water properties; however, the LC 'ageing' was mainly due to the presence of an onshore geostrophic flow from the central Indian Ocean with a maximum volume transport of 4 Sv (derived from cool, salty SICW) and the LC mixing with water from farther offshore (Smith *et al.* 1991; Woo *et al.* 2006b).

A subsurface salinity maximum recorded in the northern region (Figures 11–13), which reached the water surface south of 29.5° S (Figures 12 and 18), revealed the presence of SICW. The transition of the salinity maximum from the subsurface to the surface was rapid: the 35.7 salinity contour rose from ~150-m depth to the surface between 28 and 29.5° S. The cross-shore salinity transects 2 and 12 also showed the change in the LC between the northern and southern regions: at transect 2 (Figure 16), the subsurface core (at the 35.8-contour) had a high salinity, whereas at transect 12 (Figure 17), the salinity core was absent and the surface salinity was 35.75.

Field data obtained from the northern region revealed the presence of four surface water masses: the Leeuwin current, the Ningaloo current, the Capes current, and Shark Bay outflow (Figure 14). Field data obtained from the southern region (Figures 19 and 20) also showed the presence of four surface water masses: the Leeuwin

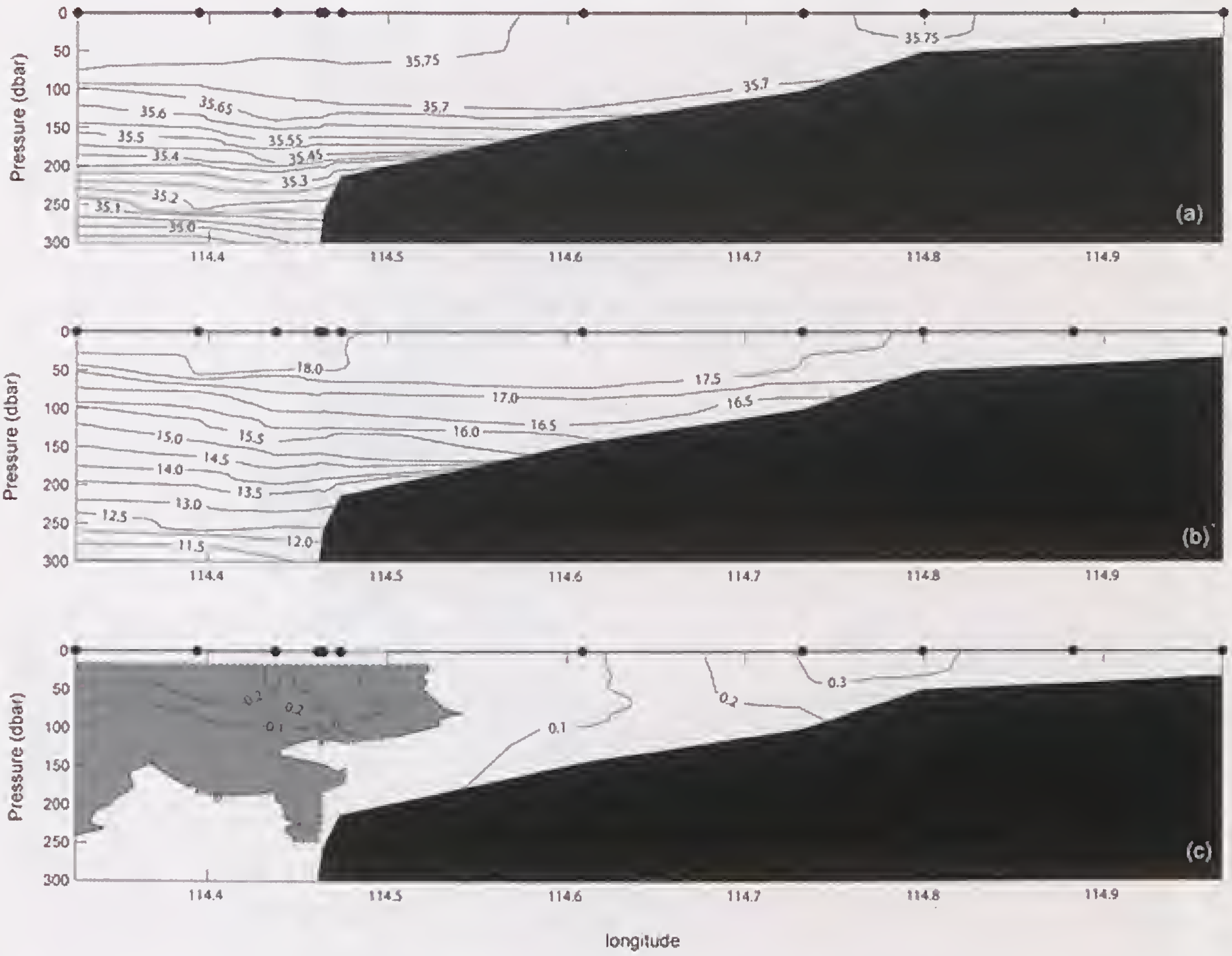

Figure 17. Transect 12 cross-sections (to 300-m depth) of salinity (a), temperature (b), and alongshore velocity (c) obtained with the ADCP. The shaded region in (c) indicates a poleward flow.

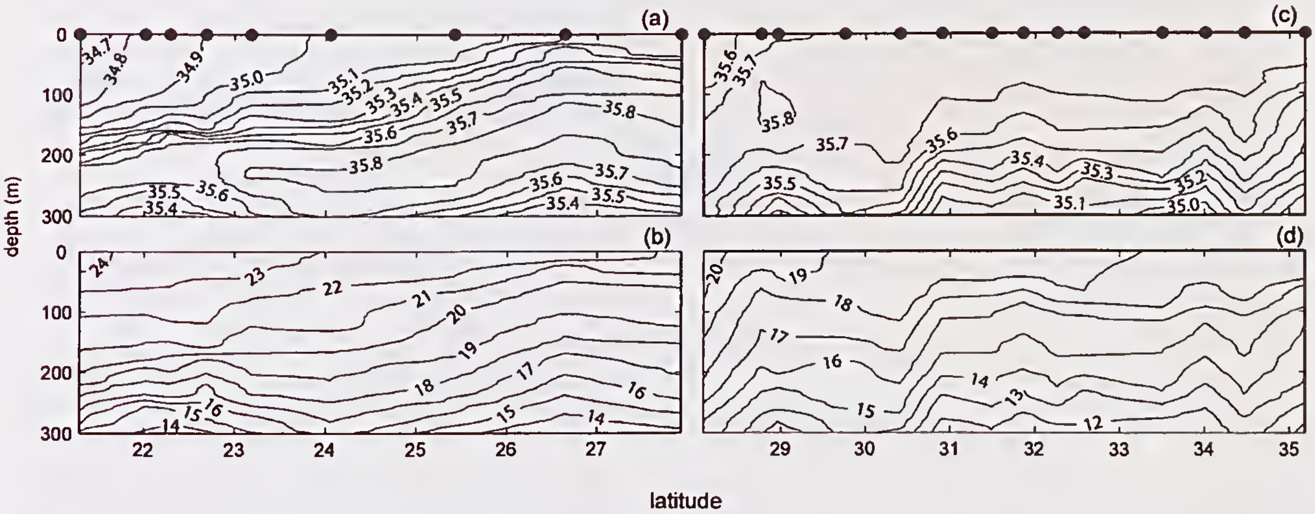

Figure 18. The alongshore transects of salinity (a) and temperature (in degrees Celsius) (b) at the 1000-m isobath for the northern region of the study area, and the alongshore transects of salinity (c) and temperature (in degrees Celsius) (d) at the 1000-m isobath for the southern region.

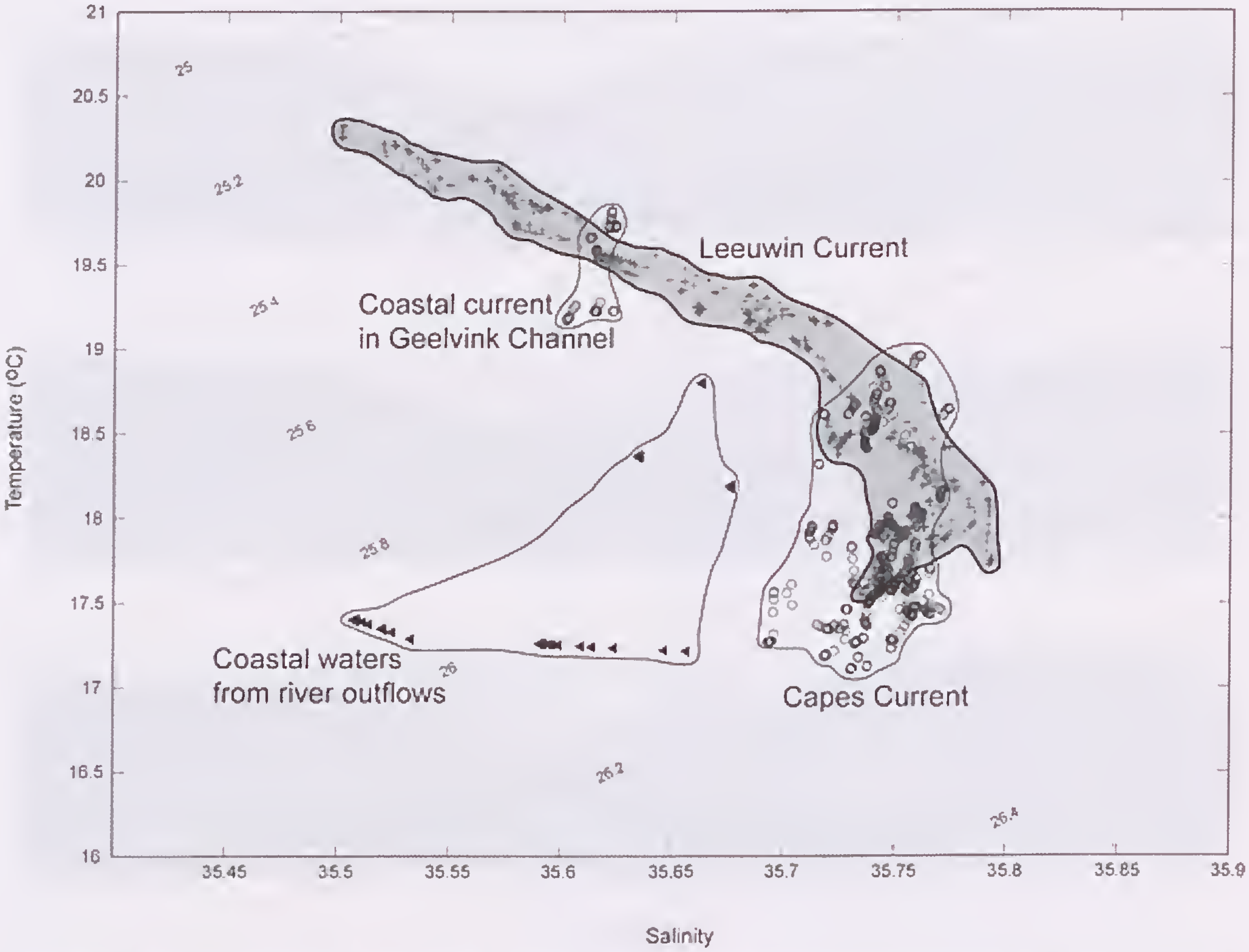

Figure 19. The temperature–salinity diagram of the surface water layer (top 100 m) from the coast to the 1000-m isobath in the southern region of the study area showing the presence of four different water masses.

current, the Capes current, water from the Geelvink Channel, and coastal waters offshore the Perth region.

The Capes current was present on the continental shelf as a continuous current from Cape Leeuwin to Geraldton (Figure 20), a distance of 750 km, and consisted of cold (17–19 °C), high salinity (35.68–35.78) water (Figure 20). The water from the Geelvink Channel to the north of Geraldton (Figure 20) overlapped with the LC, but was distinct from the Capes current (Figure 19). This water was most likely LC water that had moved onto the shelf and been changed by in situ processes. The SICW's high salinity core was located in deep water, beneath the source of the upwelling water, and thus did not introduce a salinity signature into the upwelling water. In contrast, the Capes current consisted of high salinity water because the SICW water was located at the surface.

The region offshore Perth received fresh water from estuarine and river systems such as the Swan, Peel–Harvey (Harvey and Murray rivers), and Leschenault (Capel and Brunswick rivers). The presence of cold, low salinity water at the shallow (< 50 m) stations closest to the coast showed the fresh water's effect on the coastal waters in late spring (Figure 19). Thus in a similar manner to the high salinity discharge from Shark Bay influencing the waters offshore Shark Bay, the freshwater discharge from the estuarine and river systems in the southern region influenced the shallow continental shelf waters offshore Perth. The seasonal salinity cycle at the 30-m isobath to the north of Perth also showed minimum values in September and maximum values in February, which suggested the coastal waters observed offshore Perth in the southern region were most likely a seasonal feature (Zaker *et al.* 2007).

Figure 20 shows the main features of the surface currents and associated water masses present in the southern region between October and November 2003. These recorded values reflected typical summer conditions, especially in the southern region, where strong, consistent southerly winds were experienced; however, the low salinity coastal waters were most likely absent.

The findings from the northern and southern regions can be summarised thus: the LC flowed from north to south along the 200-m isobath. Inshore of the LC, the Capes current flowed north, advecting cool, high salinity water from the south. The coastal waters offshore Perth received fresh water from estuarine and river systems,

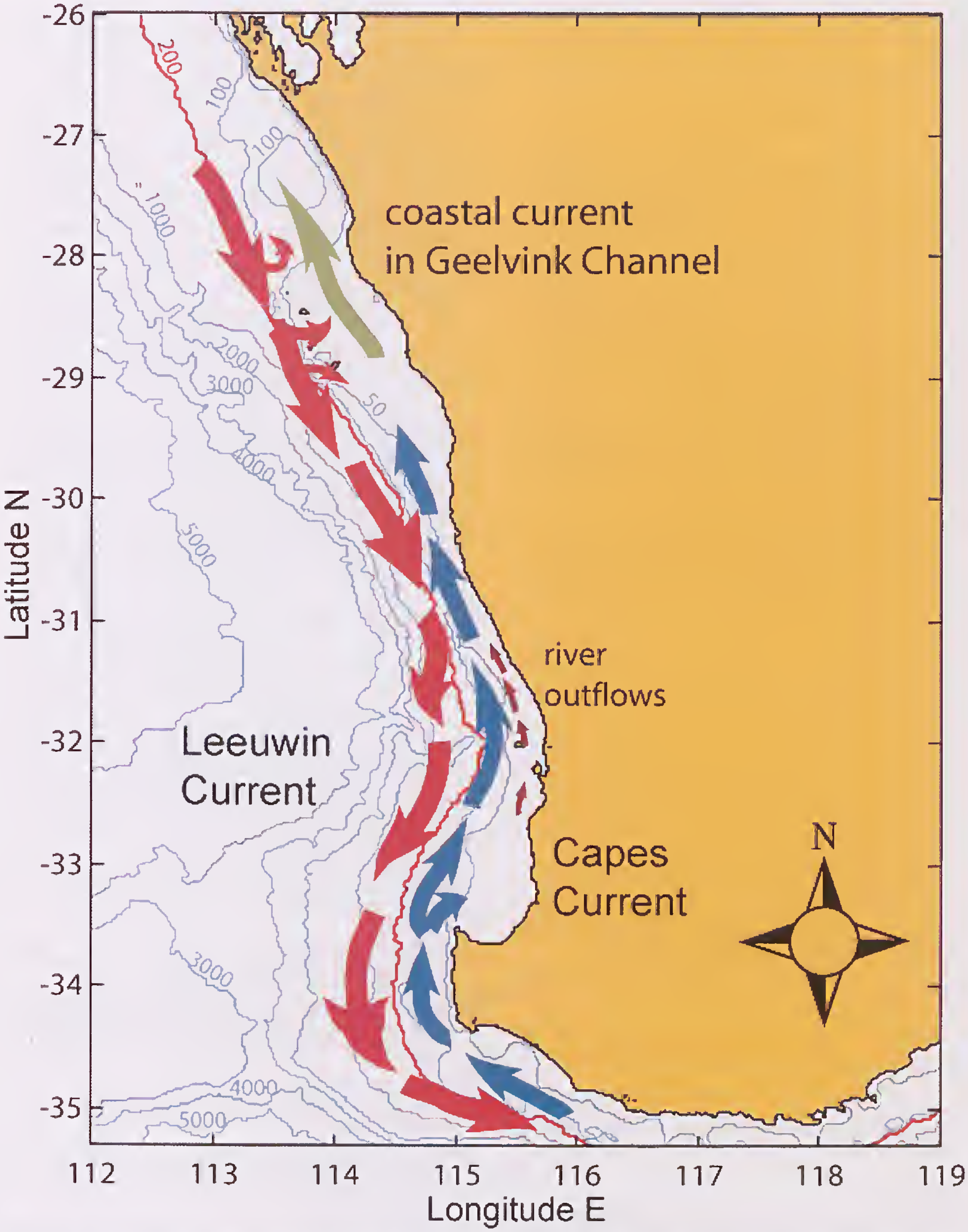

Figure 20. Schematic of the surface circulation in the southern region of the study area based on field data collected aboard the RV *Southern Surveyor*.

which lowered the salinity of the coastal waters, while localised upwelling produced a distinct water mass in the Geelvink Channel. Several water masses, distinguishable by their temperature and salinity characteristics, were present and each had a unique biological identity with different primary production regimes and phytoplankton species composition (Hanson *et al.* 2005a; Twomey *et al.* 2007).

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